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INFLUENCE OF PHYSICS ON THE DISTRIBUTION OF ICHTHYOPLANKTON ACROSS THE CHESAPEAKE BAY PLUME

by

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A Dissertation submitted to the Faculty of
Old Dominion University in Partial Fulfillment of the
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ABSTRACT

INFLUENCE OF PHYSICS ON THE DISTRIBUTION OF ICHTHYOPLANKTON ACROSS THE CHESAPEAKE BAY PLUME

Christian S. Reiss
Old Dominion University, 1997
Director: Dr. John R. McConaugha

Most marine fish have retained pelagic larval stages that are spawned away from juvenile habitats. Physical and biological processes on a number of scales may affect larval survival. Mesoscale features like estuarine or riverine plumes and fronts are thought to affect larval survival by transporting larvae to juvenile habitats or by retaining larvae in favorable developmental habitats. It is likely that these features are major contributors in the regulation of shelf-spawned estuarine-dependent taxa.

This study examined how physical oceanographic features affected the spatial distribution of ichthyoplankton across the Chesapeake Bay Plume. Larval surveys were conducted across the shelf and within the baymouth during August 1988, July and August 1992, and from July through September, 1994. Samples were collected at varying horizontal and vertical scales to understand the variability in larval distribution across the plume.

The Chesapeake Bay outflow plume and its front affected the spatial distribution of larvae and ichthyoplankton assemblages at all spatial and temporal scales sampled. The plume front delineated the seaward extent of bay-spawned taxa as exemplified by *Anchoa* spp. Multi-specific larval peaks occurred inshore and offshore of the plume front, but aggregation within the plume front itself was not observed. These multi-specific peaks consisted of pre-flexion and flexion larvae, and result from tidal oscillations of the front as

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it moves across the inner-shelf. This mechanism may retain larvae near shore, where the estuarine circulation can transport larvae into the bay.

Coastal upwelling associated with southerly winds transported plume and bay-spawned larvae to the shelf rapidly (days). Sub-surface water was transported to the coast during these upwelling events. Shelf-spawned larvae within this subsurface water were transported to the coast.

Larvae of the plume and shelf ichthyoplankton assemblages exhibited different vertical and ontogenetic distributions, across the inner-shelf. *Etropus microstomus*, a shelf-spawned and shelf-dependent taxa, exhibited differences in diel vertical distributions, and this may retain these larvae in shelf waters. *Symphurus* spp., a bay-spawned taxa exhibited an ontogenetic migration from the Chesapeake Bay plume to shelf waters, where its settles as a juvenile.

The results show that the Chesapeake Bay Plume outflow affects the spatial distribution of larval fish. The effect varies within members of an assemblage and between ontogenetic stages of some taxa. These findings support the hypothesis that estuarine plumes and mesoscale physical features may control larval survival by affecting spatial distribution.

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CHAPTER 1

Introduction

Successful recruitment of larvae to juvenile habitats is necessary for the maintenance of marine populations. Processes that occur in the early life history of fish are thought to determine year-class-strength (Hjort 1914). A major focus of larval studies has been to identify the processes responsible for density-independent fluctuations in population size related to oceanographic and environmental effects

Despite nearly one-hundred years of study, there is still a need for basic information on the patterns and processes that control larval distribution and subsequent recruitment that will result in a strong year class. The ability to predict recruitment success will help managers adjust harvest levels in order to manage fisheries in a sustainable manner. This study will investigate the importance of the physical environment in structuring the spatial distribution of ichthyoplankton across the inner continental shelf off of the Chesapeake Bay mouth

Physical Basis for Recruitment Variability

Hjorts' classic studies (1914, 1926) identified the importance of the physical environment in affecting both the biological interactions of larvae within the water column and the subsequent population densities of commercially important finfish. Examination of the age composition of spring herring, *Clupea harengus harengus*, in the North Sea

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showed that the harvest of fish in a given year was not related to differences in migration or availability to gears, but rather to year class strength. Hjort (1914) showed that survival during the larval period was important in determining year class strength. In particular he argued that there is a period just after yolk-sac absorption in which larvae could be subjected to increased mortality. Many hypotheses have tried to explain larval survival by incorporating both physical and biological processes, including the ocean-stability hypothesis (Lasker 1975,1978), the critical food (Lasker 1975) and critical food density hypotheses (Werner and Blaxter 1981), as well as the match-mismatch (Cushing 1975, 1990) and the larval retention hypotheses (Iles and Sinclair 1988)

Both the match mis-match hypothesis (Cushing 1975, 1990) and the larval retention hypothesis (Iles and Sinclair 1982) differ from the other hypotheses because they both operate at the population level and because they operate at the mesoscale. The remaining hypotheses suggest mechanisms that operate at smaller spatial scales and probably operate on cohorts or individuals within a population. In order to minimize the potential for starvation and maximize the probability of a strong year class, many fish species have evolved protracted spawning periods with episodic batch spawning in order to hedge their bets against inhospitable developmental conditions

Advection away from juvenile habitats or away from retention areas is a large source of mortality for early life stages. Adult fish have evolved behaviors that may serve to counter the effects of advection. Among these behaviors include spawning during times of peak production (Cushing 1975) or spawning upstream of juvenile nursery habitats (Harden-Jones 1968, Cushing 1990). For example, Cushing (1990) observed that sexually mature flatfish migrate out of their juvenile habitats and upstream against the prevailing

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currents in the North Sea to spawning areas. During spawning, larvae are released into the current where they are transported, passively at first, towards the Wadden Sea and their juvenile habitats. The match mis-match hypothesis, proposed by Cushing (1975), suggests that a mis-match between the timing of spawning and the seasonal primary or secondary production blooms can result in mass starvation of first-feeding larvae, thereby regulating year-class strength.

Larval behaviors have also evolved that may enhance or counter advective transport to or away from juvenile developmental habitats (Smith *et al.* 1978, Weinstein *et al.* 1980; Iles and Sinclair 1982, Stephenson and Power 1988, Perry and Neilson 1988, Sinclair 1988). Stephenson and Power (1988) found that vertical migration appeared to be the principal mechanism for retention of Atlantic herring larvae against physical advection. Weinstein *et al.* (1980) documented retention mechanisms for several estuarine-dependent fish taxa in an intensively flushed estuary. They found that some taxa remained in deep waters where the net estuarine flow could transport the larvae upstream. Other species were retained within estuaries by using selective tidal transport (rising into the water column during flooding tides and moving to the bottom during ebb tides) to counter tidal and residual flows. On the other hand the larval retention hypothesis (Iles and Sinclair 1982) proposes that retention of larvae and their appropriate prey items within tidally mixed water masses between fronts would increase larval survival resulting in strong year classes.

Large-scale climatic conditions may influence the transport and survival of larval populations (Bakun 1973, Nelson *et al.* 1977, Parrish *et al.* 1981, Norcross 1983, 1991). In the California Current System, strong year-class-strength of Northern anchovy

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(*Engraulis mordax*), has been correlated with seasons of minimal upwelling favorable winds (Parrish *et al* 1981). Similarly, correlations between Ekman transport and year-class strength have been found for winter spawning Atlantic menhaden, *Brevoortia tyrannus*, in the South Atlantic Bight (Nelson *et al.* 1977), and Atlantic croaker, *Micropogonias undulatus*, in the Mid-Atlantic Bight during late summer and early fall (Norcross 1983, 1991).

Correlations with Ekman transport alone have failed to fully predict year-class strength because the correlations did not hold over time. Therefore, additional factors are likely involved in establishing year-class strength in fish populations. Lasker (1975, 1978) investigated the role of water column microstructure on the survival of cohorts of Northern anchovy, *Engraulis mordax*. He found that stability of the water column allowed the formation of a phytoplankton maxima at the pycnocline. This maxima provided abundant phytoplankton suitable for first feeding anchovy larvae. Lasker also showed that disruption of this phytoplankton maxima following a storm resulted in starvation of the cohort.

The realization that both broad- and fine-scale physical features can affect year-class strength led investigators to examine the spatial pattern of ichthyoplankton in relation to physical processes capable of altering year-class-strength. More recent studies have incorporated studies of spawning distribution and transport phenomena as well as growth and mortality at the population level into a single focused program (Bailey *et al* 1996). Biological parameters collected in conjunction with information on mesoscale physical oceanographic features were critical in separating the importance of purely advective loss from other mechanisms of retention. These studies showed the influence of both physical

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discontinuities and behavior on the spatial distribution, recruitment, and population dynamics of pelagic and estuarine-dependent finfish. By incorporating information on eddies and secondary flows with an understanding of large scale meteorological forcing, a greater understanding of how multiple factors interact to control year-class-strength will be gained (Kendall *et al.* 1996).

Researchers have found that plankton and larval fishes are aggregated at many types of fronts. Aggregation has been reported at coastal (Iwatsuki *et al.* 1989, Nakata 1989), tidal-mixing (Pingree *et al.* 1974, Taggart *et al.* 1989), plume (Govoni *et al.* 1989, Govoni and Grimes 1992, Grimes and Finucane 1991), and estuarine (Epifanio 1987) fronts. Aggregations have also been reported for convergent flows such as langmuir circulations (Kingsford, Wolanski and Choat 1991) and internal waves (Shanks 1983, Kingsford and Choat 1986). Larval abundance within these discontinuities may be many times higher than the abundance found in the ambient water masses (Govoni *et al.* 1989, Kingsford 1990, Govoni and Grimes 1992, Grimes and Finucane 1991).

Primary (Lohrenz *et al.* 1988) and secondary production (Kiorboe *et al.* 1988, MacKinnon and Thorrold 1995) can be elevated in frontal zones as compared to inside or outside the frontal zone. It has been hypothesized that accumulated biomass at fronts might offer enhanced feeding and growth conditions leading to greater survival of ichthyoplankton (Govoni *et al.* 1989, Grimes and Finucane 1991). Increased food availability is believed to increase growth rates of larval fish, thereby minimizing size dependent mortality. Several modeling studies (Rothschild and Osborn 1988, MacKenzie and Leggett 1991) have investigated the role of increased turbulence in enhancing contact

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Table 1. Types of fronts found in ocean and coastal systems. Physical mechanism and persistence (modified from Bowman and Iverson 1977)

Frontal Type	Physical Driving Mechanism	Scale, Persistence and Examples
Planetary Fronts	Convergence through Ekman transport of large scale ocean circulation	Large scale features 1(XX)'s of kilometers in length and persisting for years e.g. subtropical convergence zone
Boundary Current Fronts	Westward intensification and poleward flow of tropical water	Large scale features 1(XX)'s of kilometers in length and of nearly constant persistence e.g. western edge of the Gulf Stream, western edge of the Kuroshio
Shelf Break Fronts	Density contrast between continental shelf and continental slope waters	Large scale features 1(X)'s of kilometers long and persisting for years, with some seasonal fluctuation in intensity e.g. Middle Atlantic Shelf Slope front, Scotian Shelf Front
Upwelling Fronts	Offshore directed Ekman transport of coastal waters in response to alongshore wind-stress	Large scale features 1(X)'s of kilometers in length with strong seasonal signal, common to Western Continental Boundaries e.g. California Current System, Peruvian coast, and the Benguela current system
Shallow Sea Fronts	Tidal mixing of shallow shelf waters creating a density difference between shallow and deep areas	Mesoscale features 1(X)'s of kilometers in length, seasonally persistent, with significant spring neap modulation of position e.g. Irish Sea, and English Channel
Plume Fronts	Density difference driven by seaward flowing river or estuarine discharge to the coast	Mesoscale features ranging from 10-1(X)'s of kilometers with strong seasonal, and tidal signals e.g. Mississippi River Plume Front, Columbia River Plume, Amazon River, **Chesapeake Bay outflow plume**
Estuarine Fronts	Density contrast between estuarine waters due to mixing, warming or longitudinal shear of tidal currents	Mesoscale features ranging from 10's - 1(X)'s of meters, with very periodic occurrences associated with tidal ebb and flood cycles e.g. Bowden Reef, GBR, Charleston Harbor, USA, Chesapeake Bay Mouth, USA

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rates between fish and their prey The results of these studies support the hypothesis that small scale mixing at frontal interfaces may increase larval survival by increasing the encounter rates between ichthyoplankton and their prey items (Rothschild and Osborn 1988; MacKenzie and Leggett 1991). Results of field studies that have examined feeding success within and around fronts have been equivocal Govoni and Chester (1990) and Powell *et al.* (1990) found no differences in the percentage of starved larvae or in the feeding responses of larvae of a variety of species aggregated at the Mississippi River plume front. On the other hand, Kiorboe *et al.* (1988) found that in some instances larvae grew more rapidly in frontal zones than in other water masses

Along frontal transport occurs at frontal zones, and this transport has been hypothesized to function as a transport pathway for estuarine-dependent larvae (Shaw *et al.* 1985; Nakata 1989). Shaw *et al.* (1985) found significant alongshore transport of Gulf menhaden, *Brevoortia patronus*, within an area of stratified water inshore of mixed shelf waters They hypothesized that transport within this boundary layer could play an important role in the successful transport of these larvae to juvenile habitats downstream Nakata (1989) and Govoni *et al* (1989) placed drifters on either side of a coastal front and tracked the movement of eggs and larvae in the vicinity of the drifters Eggs and larvae were transported at different rates and in different directions, retaining some eggs and early larvae in the vicinity of the coastal front and coastal embayments, while others were advected away from coastal embayments The differential advection observed across the front may be important in transporting larvae to or retaining some larvae within appropriate habitats

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Frontal Dynamics

Bowman and Iverson (1978) reviewed the physics of different types of fronts They classified oceanic fronts into seven types based upon the driving mechanism, length scale and persistence (Table 1). These range from large scale fronts separating oceanic water masses, with length scales of thousands of kilometers and persisting for years, to small scale estuarine fronts with length scales of 100's of meters and persisting for just a few hours. In general, fronts are formed by a pressure gradient driven by density differences between two water masses The density gradients arise from differences in salinities or temperature, as in riverine or estuarine fronts (Garvine 1974, Garvine and Monk 1976, Bowman *et al* 1978) or they can also arise from tidal energy and topographic features. This energy mixes water over shoals creating a front between the mixed water and the stratified water (Pingree 1974, Lefevre 1986, Simpson and James 1986) Finally, fronts can also result from shear between two different areas, as in shoals and channels While the driving forces and length scales of these fronts are different, there are several features common to almost all fronts Fronts are delineated by compressed horizontal changes in some water properties At the front, convergence of water masses results in downwelling and increased small-scale mixing (on the order of meters) between the two water masses, while also forming a boundary between the masses at larger scales (kilometers).

In riverine plumes the gradient in properties arises from the outflow of freshwater onto a shelf of more saline water A pressure gradient arises from the outflow of this light water out over the ambient coastal water mass (Garvine 1974, Mann and Lazier 1991) As the plume spreads seaward it mixes at the pycnocline and slows as a result of friction A

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front is formed where seaward spreading and downward mixing are equal (Garvine 1987). Garvine (1987) and Chao and Boicourt (1986) have both modeled the outflow of freshwater onto the shelf from large outflows like the Chesapeake Bay. Their results are similar to previous observations made at river plume fronts (Garvine 1974, Bowman and Iverson 1978). Outflowing plume water in wide rivers or estuaries (like the Chesapeake Bay) responds to the Coriolis force, turning to the right (northern hemisphere) and becoming a coastally trapped current with a front on its seaward edge.

Many river plumes are shallow (<5m), and are therefore not affected by bottom friction (Wong and Munchow 1995). This allows riverine plumes to respond to tidal and meteorological forcing without the influence of bathymetry (Boicourt *et al* 1987, Wheless 1993). Boicourt *et al* (1987) and Johnson (1985) found that the Chesapeake Bay plume responds rapidly to shifts in the wind by compressing against the coast in response to northerly winds or expanding seaward under influence of the southerly winds. A similar response to tides has been observed in the Chesapeake Bay outflow plume, where it expands seaward on ebb tides and contracts towards the coast on flood tides (Wong and Munchow 1995, Valle-Levinson and Lwiza 1996). Wiseman and Garvine (1995) indicated that the dynamic nature of riverine plumes and fronts, especially the response to episodic events, was critical in understanding the flux of nutrients and buoyancy to the shelf.

One of the more noticeable physical features on the continental shelf off Virginia is the Chesapeake bay plume. The Chesapeake Bay plume and front are features that may influence the survival of estuarine-dependent larvae because it lies between the spawning areas on the shelf and the nursery habitats within the bay. Estuarine-dependent larvae must move through, under, or around the plume to gain access to the Chesapeake Bay. Among

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these estuarine-dependent taxa are Atlantic croaker (*Micropogonias undulatus*), and Spot (*Leiostomus xanthurus*). These species are responsible for most of the commercial harvests of finfish in the Virginia portion of Chesapeake Bay. In addition, ecologically important taxa like *Anchoa* spp. are found on the inner shelf and within the Chesapeake Bay outflow plume where they may compete with commercially important taxa for food and are important prey species for many adult fish taxa. An understanding of the influence of the Chesapeake bay plume front on the distribution of ichthyoplankton may lead to insights regarding fluctuations in year-class strength due to advective loss, or predator-prey interactions at the front.

Physical Setting

Circulation in the Middle Atlantic Bight (MAB) is dominated by an alongshore current that flows from the northeast to the southwest, and is affected by winds, and freshwater outflow from three principal sources, the Hudson River, the Delaware Bay outflow, and the Chesapeake Bay outflow. The physical oceanography and circulation of the Mid-Atlantic Bight (MAB) has been examined by Iselin (1955), Beardsley *et al.* (1976) and Bumpus (1973). Iselin (1955), examined temperature and salinity profiles across the shelf of the MAB and found that temperature decreased and salinity increased with distance offshore and with depth. He proposed that the entire shelf acted as an estuary with warm fresher water moving down the coast and offshore at the surface, while cold salty water moved towards the coast at depth. Drifters released by Bumpus (1973) showed that the mean alongshore current was southwestward at about 2 cm/s nearshore and increased to about 5 cm/s offshore. Few drifters released over the outer shelf were recovered and he concluded that significant eastward transport of shelf water occurred.

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supporting the general premise of an estuarine type circulation on the MAB shelf Beardsley *et al.* (1976) estimated that the mean flow and volume transport in the MAB were similar in direction and magnitude and supported the conclusions of Iselin (1955) and Bumpus (1973).

Beardsley *et al.* (1976) and Beardsley and Butman (1974) studied changes in current velocity on the shelf during stratified (summer) and unstratified (winter) conditions. They suggested that during stratified conditions the currents were dispersive and reacted to meteorological forcing rather than flowing with the net alongshore current During unstratified conditions, Beardsley and Butman (1974) found that meteorological forcing produced coastal water setup during northeasterly winds and setdown during southwesterly winds. The resulting alongshore current was barotropic

Another important feature within the MAB is the presence of a cold pool of water on the outer shelf. This water mass is a remnant of seasonally produced, cold, winter water. It is trapped at depth near the shelf edge by increased insolation of surface water and decreased mixing during spring. Cold pool water (CPW) is distinguishable from surrounding waters because of its lower temperature, 7-8 °C (Bigelow 1933). Houghton *et al.* (1982) found that CPW was a continuous feature that travels southwest along the shelf edge at the speed of the mean shelf current (5 cm/s). They found that CPW plays an important role in the heat budget of the MAB cooling the water rapidly during the fall overturn

During summer, when the water column in the MAB is stratified, prevailing southwesterly winds can induce significant coastal upwelling. Coastal upwelling is transient, but greatest during July and August (Johnson and Hester 1989). These

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southwesterly winds (upwelling favorable) result in significant offshore transport of surface waters (Bowman *et al* 1978). As a result of offshore transport of surface water, sub-surface CPW moves from the mid-shelf to the shore rapidly (within 24 hours) (Hicks and Miller 1980) in response to continuity requirements. These same winds can induce a coastal counter-current in surface waters (Bowman *et al.* 1978, Johnson 1987). Johnson (1987) deployed current meters off the Chesapeake Bay mouth and documented this counter current as having a mean northeastward current of 5-15 cm/s just east of the Chesapeake Bay plume outflow.

Chesapeake Bay

The mean estuarine outflow of the Chesapeake Bay is approximately 10,000 m^3/s (Arnoldo Valle-Levinson pers. comm.) and undergoes a seasonal cycle with maximal flows during the spring freshet and minimal flows during August and September. The estuarine outflow is roughly 4 times the river flow, and is highly modified by wind and tide. The mean tidal amplitude is approximately 2m and the tides are semi-diurnal.

The baymouth is 29 km wide and has a mean depth of 10m with three main navigation channels with depths in excess of 20m. These channels are nearly equally spaced across the bay-mouth and form a complex area of shoals and channels with strong shear fronts marking the transition between areas (LaCouture 1983 after Oertel).

Circulation in the Bay mouth is complex, changes in circulation occur on daily and seasonal time-scales. The principal flow is estuarine. The inflow is generally concentrated within the deep channels while net outflow occurs on both the southwestern side of the bay (Cape Henry) and northeastern side of the bay (Cape Charles) as well as over shoals (Boicourt 1981). These areas of mean outflow are modified by the spring-neap cycle such

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that net inflow (in sub-surface waters) occurs during neap tide periods (Valle-Levinson 1994). Local southerly winds pull water out of the bay, while increasing the sub-surface inflow, and northerly winds act to transport water into the bay in both surface and sub-surface waters.

Ocean-estuary coupling (Wong and Munchow 1995), estuarine outflow (Wang 1979; Wang and Elliott 1978; Valle-Levinson 1994), plume-shelf interactions (Boicourt 1981; Boicourt *et al.* 1987) and shelf-slope exchange (Boicourt and Hacker 1976, Flagg *et al* 1994) also respond to meteorological forcing Within the southern MAB, all these features become important and are reinforced by the presence of the large outflow of relatively fresh water from the Chesapeake Bay Based upon drifter and bottle returns, Norcross and Stanley (1967) found that sub-surface waters were transported into the Chesapeake Bay from up to 50 nmi seaward of the bay mouth Drifters released seaward of 70 km were generally not recovered and those that were recovered were found along the Outer Banks of North Carolina More recent studies of coastal circulation in the baymouth region (Boicourt 1973) found that during periods of significant runoff, the Chesapeake Bay outflow plume was detectable as far south as Cape Hatteras, NC and well seaward of the coast Studies by Boicourt (1981) and Johnson (1987) which used current meters to examine exchange at the baymouth, revealed complex interactions between bathymetry and estuarine outflow as well as between wind strength and the direction of near-coastal surface circulation (Johnson 1987) Boicourt *et al.* (1987) found significant wind-mediated effects for both the plume outflow and its associated front, and for heavier coastal water that moved into nearshore areas during upwelling favorable conditions

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Two studies have examined transport into and out of the Chesapeake Bay and have found evidence for significant ocean-estuary coupling in the form of coastal water setup and setdown in response to non-local forcing (Wang 1979, Wang and Elliott 1978) Over long time scales (>20 days) non-local forcing was more important than local meteorological conditions on volume exchange into the estuary At higher frequencies (2 5 to 5 days) local forcing was more important. Similar findings were detailed by Wong and Munchow (1995) for the Delaware Bay mouth

Aim of this Dissertation

Estuarine and riverine plumes and fronts may partially control the spatial distribution of ichthyoplankton taxa and assemblages (Govoni *et al* 1989, Grimes and Kingsford 1996) How these mesoscale features affect the dispersal, recruitment and survival of ichthyoplankton is still unresolved, and studies to determine their importance are needed (Kingsford 1990) This dissertation will investigate the role of physics, principally plumes, fronts and meteorological forcing, on the distribution and structure of ichthyoplankton assemblages across the Chesapeake Bay plume front and the inner continental shelf Indicator taxa representative of the plume and the shelf are derived, and then used to explore the consequences for larval dispersal, recruitment, and survival of several different taxa

The horizontal and vertical distribution of indicator taxa is examined in relation to plume, frontal and shelf zones in chapter 2 These analyses show how the assemblages are delineated on a broad spatial scale Differences in vertical distribution between daytime and nighttime were examined to investigate how larvae may be retained in appropriate developmental zones against the net estuarine and long-shore circulation Ontogenetic

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changes in assemblage membership are also described

Chapter 3 investigates the cross-frontal distribution and relative density of ichthyoplankton taxa along a transect from the baymouth to the inner shelf during summer. Correlations between the density of overall ichthyoplankton and several indicator taxa with both physical oceanographic and meteorological factors are performed to determine whether the Chesapeake Bay plume front aggregates larvae or functions to separate larval assemblages from the shelf and plume

Chapter 4 examines larval abundance and depth distribution across shear fronts produced by differential advection in channels and over shoals within Chesapeake Bay Cross-frontal ichthyoplankton distributions are examined relative to the shear front to see if these fronts aggregate larvae and whether distinctive larval assemblages are retained as the larvae are transported into the Chesapeake Bay

The role of summer upwelling events in restructuring of ichthyoplankton assemblages associated with plume and coastal waters is explored in Chapter 5 Cross-shelf transport of the plume assemblage is documented and the time scale for offshore transport is discussed

The goal of the studies and analyses was to understand how larvae are retained or dispersed in relation to riverine plumes and fronts, in order to explore whether these physical features affect survival of ichthyoplankton taxa Such determinations are necessary for the development of realistic models that can predict recruitment success Patterns in the spatial distribution of *M. undulatus* are related to the hypothesized recruitment pattern for *M. undulatus* developed by Norcross (1983, 1991) in light of historical and new data in chapter 6

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Indicators of Larval Assemblages

In order to simplify the study of the plume and it's front on the distribution of ichthyoplankton a few species were selected as indicator taxa representative of the plume and shelf assemblages. The effects of physics on the spatial distribution of these indicator taxa was compared to other assemblage members, to determine how individual taxa may differ.

Determination of Indicator Taxa

Two taxa representing the plume and the shelf assemblages were chosen after considering both adult spawning seasons and their spawning distributions on the shelf off of Virginia. Potential indicator taxa were determined using criteria described by Laws (1993). Principal ichthyoplankton assemblages were identified from inner shelf samples using multivariate ordination techniques (Gauch 1982). The primary function of the multivariate ordination (Principal Component Analysis) was to show that the assemblages did not overlap, so that potential indicator taxa would represent different larval assemblages (plume and shelf). The samples used for identification of indicator taxa were collected during late July 1992 from a series of stations located on the inner shelf adjacent to Chesapeake Bay (see chapter 2 for detailed sampling procedures).

PCA resolved two clear assemblages of larval fish whose taxa did not vary between day and night (Fig. 1). The two assemblages represent taxa spawned within the lower bay or the plume, and an assemblage composed of shelf-spawned taxa. These derived assemblages closely resemble the plume and shelf assemblages derived by Olney (1996). Five of the thirteen taxa used in the analysis were eliminated from consideration as potential indicators because they showed variability in their position in the PCA between

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daytime and nighttime suggesting that they were not tightly correlated with the underlying environmental gradients (Fig. 1). Of the remaining eight potential indicator taxa, three taxa were members of the plume assemblage and five were members of the shelf assemblage

Symphurus spp. was eliminated from consideration as an indicator of bay or plume spawned taxa because there is confusion as to which assemblage this taxon belongs Based upon the study by Olney (1976), *Symphurus* spp seems to be spawned within the baymouth and is a member of the plume assemblage However, in a later study by Olney (1996), *Symphurus* spp. was associated with the shelf assemblage Therefore this taxa was not considered to be a suitable indicator *Menticirrhus* spp was eliminated because this taxa was not abundant relative to either *Symphurus* spp or *Anchoa* spp Laws' criteria suggests that an indicator organism should be abundant relative to other taxa in the assemblage that it represents

Of the three members of the plume assemblage defined by PCA, only *Anchoa* spp remains as a potential indicator for the plume assemblage While comprising three separate species in the Middle Atlantic Bight, *Anchoa* spp meets many of the criteria set for an indicator taxa. *Anchoa* spp are the most abundant taxa captured within the plume and the baymouth during summer (Olney 1983) The larvae of all three taxa are spawned during the summer and the most common form, *Anchoa mitchilli*, spawns from about April through September This time period encompasses the spawning period of the other two taxa forming the group (Fahay 1983) Additionally, the larvae of *Anchoa* spp are easily identified, an important criteria for an indicator organism These larvae are not known to be spawned in shelf waters and therefore early stage larvae would not be present in shelf waters unless transported there by some physical mechanism

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Of the five members of the shelf assemblage that may be representative of shelf waters, *Ophidion* spp. and *Peprilus triacanthus* were eliminated because they are less numerous than either *E. microstomus*, *Prionotus* spp. and *C. striata*. In addition, *Prionotus* spp. was eliminated because the early larvae are not easily distinguished and the larvae may occur in estuarine and coastal waters (Fahay 1983, McBride and Able 1994).

The remaining two taxa, *C. striata* and *E. microstomus* both spawn throughout the MAB between July through September (Fahay 1983), and their larvae are abundant and are easily identified. The center of the range of *C. striata* is north of the Chesapeake Bay and this may affect the year to year abundance of *C. striata* if advection affects their abundance on the Virginia shelf. Therefore *C. striata* not considered to be a reliable indicator of shelf-spawned taxa.

Etropus microstomus is the only taxa that is abundant enough to reflect the distribution of the shelf assemblage. This taxon spawns from July through September within the Middle Atlantic Bight, inside of the 60m isobath (Richardson and Joseph 1973). The larvae are relatively easily identified at small sizes (pre-flexion). Further, there are no other species of *Etropus* known to spawn north of Cape Hatteras. Although *Etropus cyclosquamous* and *E. crossotus* spawn south of Cape Hatteras their larvae may be transported to the MAB with the Gulf Stream, and may be found occasionally on the Virginia shelf as expatriates. Occurrence of these expatriates would not effect overall density estimates of *E. microstomus* because the abundance of expatriates would be low. Furthermore, since all *Etropus* spp. would occur in shelf waters, determination of the shelf assemblage would not be compromised by their inclusion.

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Anchoa spp., and *E. microstomus* will be used as indicators of the plume and shelf assemblages, respectively. Throughout this study, comparison between the shelf indicator (*E. microstomus*) and a commercially important shelf-spawned taxa, *M. undulatus* will be made to understand whether the current recruitment paradigm described by Norcross (1983, 1991) and Norcross and Austin (1988) may need revision and refinement. Likewise, comparisons between the distribution of *Symphurus* spp. with both *Anchoa* spp., and *E. microstomus* will be made to assess the effects of physics on the distribution of this taxa in light of work that has suggested that *Symphurus* spp. is spawned within the Bay (Olney 1976) and yet is a member of the shelf assemblage (Olney 1996).

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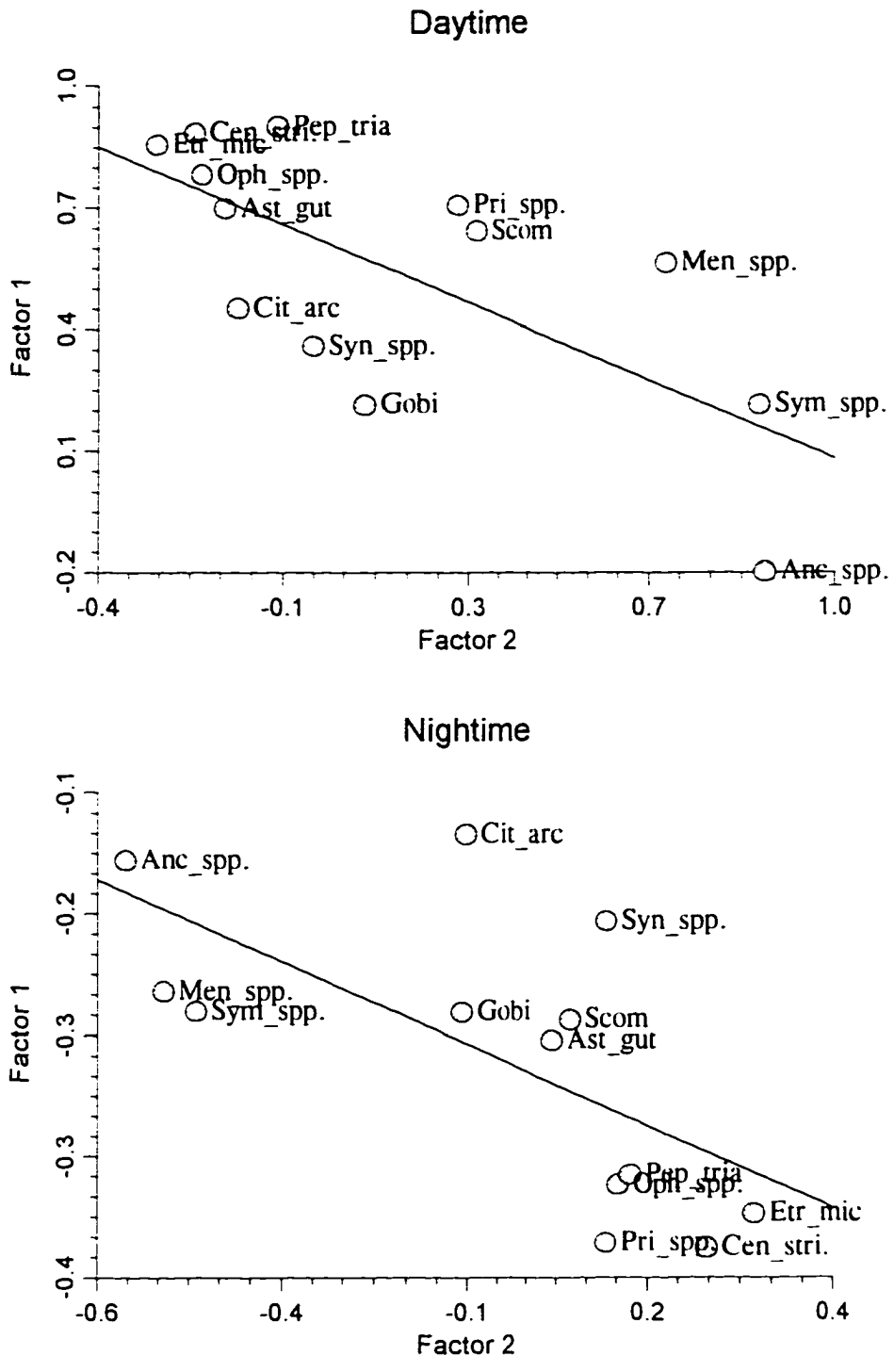

Figure 1. Factor loadings plots of day-time (a) and night-time (b) PCA results. The lines are regression lines that are significant (α <0.01). The two end-members of these ordinations represent the plume and the shelf assemblage, and are indicated by *Anchoa* spp. (the plume), and *Etropus microstomus* (the shelf).

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CHAPTER 2

Horizontal and vertical mesoscale distribution of ichthyoplankton across the Chesapeake Bay Plume: ontogenetic changes in assemblage membership

Introduction

Riverine plumes and fronts are important features in the coastal ocean because they are areas of convergence, delineate water masses and lie between the estuary and the shelf (Bowman and Iverson 1978). Both shelf-dependent and estuarine-dependent larvae may be aggregated within these features (Kingsford 1990, Grimes and Kingsford 1996). For shelf-spawned estuarine-dependent taxa, some mechanism or behavior may be required to circumvent the plume and successfully recruit to estuarine habitats.

Little information is available on the horizontal and vertical distributions of ichthyoplankton near plume fronts. Most studies have compared densities of larvae in the plume, frontal and shelf waters and focused on the surface because of the convergent nature of the flows there (Govoni *et al.* 1989, Govoni and Grimes 1992, Grimes and Finucane 1991, Kingsford 1990, Kingsford and Suthers 1994). Other studies examined the composition and distribution of larval assemblages across frontal zones using oblique tows that integrated vertical differences in larval distribution (Richardson and Pearcy 1977, Richardson *et al.* 1980, Sabates 1990, Sabates and Olivar 1996). In one of the few studies

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that examined cross-frontal distribution in relation to depth. Moser and Smith (1993) showed that the vertical distribution of ichthyoplankton may change across open ocean fronts. They suggested that larvae respond to changes in the trophic conditions related to upward sloping chlorophyll-a isopleths. Govoni *et al.* (1989) however, was unable to find any consistent effect between several fish taxa, the Mississippi River plume front and depth. They attributed this to the dynamic nature of this frontal zone

Differences in vertical distribution of larval fish may be caused by physical mechanisms, behavioral responses, or both. These migrations and changes in vertical position may enhance survival by placing larvae in favorable advective flows or by retaining larvae in favorable feeding or developmental habitats (Smith *et al.* 1978, Weinstein *et al.* 1980; Southward and Barrett 1983, Brewer and Kleppel 1986, Perry and Neilson 1988, Stephenson and Power 1988, Cho 1996). Significant changes in diel vertical distribution of a variety of larval fish have been reported in Middle Atlantic Bight shelf waters (Smith *et al.* 1978; Kendall and Naplin 1981). Larvae were found at the surface at night, and occurred at or below the thermocline during the day. Vertical migration of larvae may be in response to light, tides or predator-prey fields (Neilson and Perry 1990). Smith *et al.* (1978) and Kendall and Naplin (1981) suggested that vertical migration may be important to feeding and predator avoidance. Cho (1996) hypothesized that these changes in vertical distribution could result in transport to, or retention in, favorable shelf habitats in the Middle Atlantic Bight

Differences in the suite of responses elicited from larvae that encounter advective or dispersive environments are closely tied to length. For example, small Atlantic croaker (*Micropogonias undulatus*) larvae occurred in the mid- to upper water column. Larger

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larvae are found deeper in the water column where they may be entrained by the estuarine flow (Weinstein *et al.* 1980; Norcross 1983, 1991) Understanding the ontogenetic distribution may help to elucidate how fronts affect larval survival and recruitment

This study has three goals. The first is to derive and ordinate larval assemblages representative of the plume and the shelf. From these derivations, indicator taxa for the plume and shelf assemblages will be selected using the criteria defined in chapter 1. Next, mesoscale the horizontal and vertical spatial distributions will be examined in relation to time of day to determine whether there are differences between plume and shelf taxa Finally, this study will examine whether different members of the same assemblage exhibit different distributional patterns The horizontal and vertical distributions of a known estuarine-spawned taxa, *Symphurus* spp., that is found as part of the shelf assemblage (Olney 1996) will be examined Specifically the hypothesis that ontogenetic migration is responsible for the difference in horizontal and vertical distribution will be tested This study of horizontal and vertical distribution of larvae from the plume and the shelf will help to clarify the role of the plume front on larval survival by retention in appropriate developmental habitats

Oceanography of the inner shelf

The oceanography of the Mid-Atlantic Bight on the Virginia shelf is dominated by the presence of two water masses, Mid-Atlantic Shelf water that has salinities in excess of 30 psu and ranges from 30-34 psu (Manning 1991), and Chesapeake Bay plume outflow water that has salinities considerably <30 psu (range from ~15 to 25 psu in the baymouth) (Boicourt 1981)

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The Chesapeake Bay plume flows onto the shelf and turns south in response to the Coriolis force (to the right in the northern hemisphere), resulting in a coastally trapped current. The bathymetry of the inner shelf is simple, with few channels or other bathymetric features that can steer circulation. The outflow plume drives a considerable estuarine circulation on the inner shelf that transported bottom drifters into the bay from up to 50 km offshore (Norcross and Harrison 1967). Such an estuarine circulation could be a powerful mechanism in the transport mechanism for estuarine-dependent larvae

On the shelf, plume position and strength are modified by wind forcing, tidal conditions, and river flow (Boicourt 1981; Boicourt *et al.* 1987). The seaward edge of the outflow plume forms a front that separates the bay water from the shelf water. Separation of the two water masses is not complete, and the front is characterized by intense mixing.

Materials and Methods

Ichthyoplankton were sampled over a 72 hr period at 28 stations over the inner Virginia shelf between July 26-29, 1992. Transects were spaced at 7.5 km intervals between the (baymouth) 37^0 05'N and 36^0 40'N (Fig. 2). Stations were equidistant along each transect. However, as a result of naval operations in the sampling area, two stations were not sampled and many of the stations were not sampled in order.

Temperature and salinity (as conductivity) were measured at each station using a Seabird SBE-25e CTD. Because of electronic failure of the conductivity cell on the CTD, it was not possible to determine the salinity at many stations. As a first order measure of potential food, water samples for chlorophyll-a analysis were collected with 5 liter Go-Flo bottles at alternating stations. Two sub-samples were obtained for each depth (5m intervals to 20m). Chlorophyll-a samples were frozen and then analyzed fluorometrically

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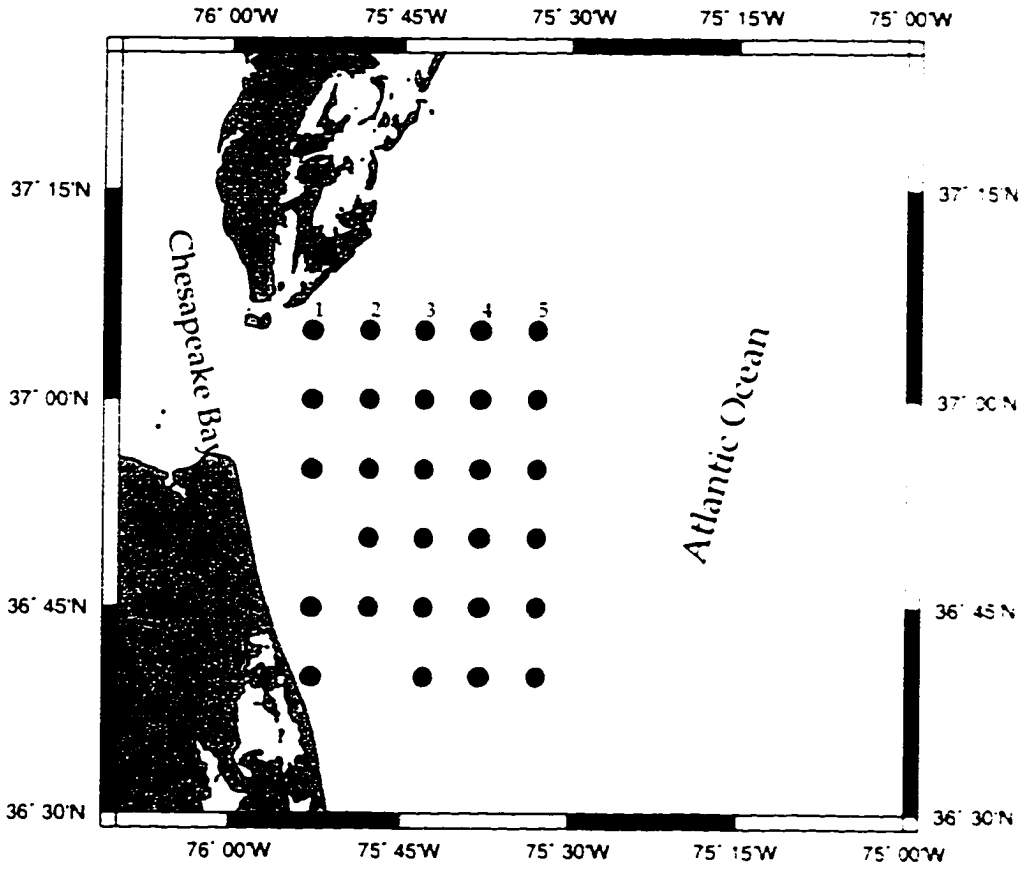

Figure 2 Map of sampling stations on the Inner Continental Shelf off of the Chesapeake Bay mouth occupied from July 26-29, 1992

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using the methods of Parsons *et al.* (1984).

Ichthyoplankton samples were collected at 1m, 3m, 7m, and 9m with a 75-cm opening and closing bongo net fitted with 333μ mesh and equipped with General Oceanics model 2030 mechanical flowmeters. *In toto*, 97 ichthyoplankton samples were collected.

Plankton samples were initially preserved in 10% formalin and later transferred to 70% ethanol for storage. Ichthyoplankton were removed from all samples and sub-sampled with a Folsom plankton splitter when samples had exceedingly high concentrations of larvae (usually inshore samples dominated by *Anchoa* spp.). Sub-samples were never less than 1/4 of the sample. In each case, the entire sample was examined for large and rare individuals. All ichthyoplankton were identified to the lowest possible taxon and densities of larvae are reported as #/100m^3. Larvae of selected taxa were measured to the nearest 0.1 mm (total length for pre-flexion, standard length for post-flexion) using the OPTIMAS Image Analysis System and then grouped in 1mm increments for analysis. No correction for shrinkage was applied.

Data Analysis

Samples were assigned to daytime or nighttime groups based on time of day; samples collected between 2000-0600 hr were assigned to night. Only larval taxa that occurred at densities >1.0/100m^3 in both the daytime and nighttime samples were used in the analysis. Principal Component Analysis (PCA) (NCSS, Kaysville, UT) was applied to a Pearsons correlation matrix (species X sample) of log-transformed ln(x+1) abundance data of both daytime and nighttime samples, *sensu* Sabates (1990) and Richards *et al.* (1993). Thirteen taxa common to both daytime and nighttime samples were used. Data were standardized by subtracting the mean of the daytime or nighttime stations from each

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datum. Factor loadings greater than 0 5 were used to define assemblage members Derived assemblages were compared graphically Linear regression was used to determine if the relationship between the first and second factor loadings was random with the assumption that the slope of a random ordination would be zero Representative taxa (indicators) for the plume and the shelf assemblages were selected applying the criteria described in chapter 1

The lack of a complete salinity dataset for the cruise complicated the identification of plume, frontal and shelf waters. In order to determine the relative position of these water masses, a surface and 5m contour map of chlorophyll-a was derived by kriging the discrete concentrations to delineate zones (SURFER, Golden Software) Although chlorophyll-a is a non-conservative environmental parameter, previous studies (Robertson and Thomas 1981, Reiss chap 3) have shown that there is a significant decline in chlorophyll-a concentration across the front, and that values >0 5 μg L and <1 5 μg L were consistently associated with frontal waters at the Chesapeake Bay mouth Based on the spatial distribution of surface chlorophyll-a concentrations and the relationship between chl-a concentrations and frontal waters, stations were assigned to one of three "zones", plume, frontal and shelf

General linear models (GLM) ANOVA methods were used to examine the effect of three factors time of day, location (plume, frontal, shelf), and depth on the spatial distribution of larvae Data were rank transformed to stabilize the variance and remove problems associated with skewed abundance (Conover and Iman 1981) Tukey-Kramer multiple comparisons procedures were then performed on the ranks

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Ontogenetic differences in cross-shelf distributions of *Anchoa* spp., *E. microstomus* and *Symphurus* spp. larvae were examined by plotting the distribution of larvae by length class. Each taxa was partitioned into three length classes, <3.5 mm, 3.5-7.0 mm, >7.0 mm. An extra length class, >10.0 mm was also used for *E. microstomus*. Length classes were taken from the published literature and reflect major divisions in larval ontogeny, principally pre-flexion, and post-flexion. Eye migration in the flatfish was also used as a significant ontogenetic stage (Fahay 1983).

Identification of the early stages of these taxa is problematic, and some qualifications of the species determinations are required. Three species of *Anchoa* spp. are found within the Middle Atlantic Bight. On the Virginia shelf the dominant species is *Anchoa mitchilli*. *Anchoa* spp. will be used in this study (Olney 1983). *Etropus microstomus*, a shelf-spawned shelf-dependent taxa, is the only member of this genera that is known to spawn north of Cape Hatteras. At least two other species of *Etropus*, *E. cyclosquamous* and *E. crossotus* are at times found in limited numbers north of Cape Hatteras (Richardson and Joseph 1973). *Etropus microstomus* is expected to be the overwhelmingly dominant form of this genera within the sampling area and all larvae of this genera will be considered *E. microstomus*. More than one species of *Symphurus* spp. occurs in the mid-Atlantic Bight, but larvae of these species are not well described. *Symphurus plagiusa*, is the dominant form *Symphurus* spp. in Chesapeake Bay (Olney 1976). For the purposes of this study all larvae will be grouped together under *Symphurus* spp.

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Results

Distribution of chlorophyll-a and identification of hydrographic zones

Surface chlorophyll-a concentrations decreased across the sampling area and were highest inshore south of the Chesapeake Bay mouth (Fig. 3a). Low chlorophyll-a concentrations (<0.5 μg/L) were present in southern, offshore areas. This low chl-a area represents shelf water that has not been diluted by high chl-a plume waters. There were no offshore peaks in chlorophyll-a in the surface waters of the inner shelf that would suggest that chl-a is being concentrated in a broad zone of convergence. The cross-shelf distribution of chl-a at 5m was similar to the pattern observed for the surface, although intermediate concentrations (0.5-1.5 μg/L) were found over more of the sampling area (Fig. 3b).

The cross-shelf sections of chl-a concentration showed a pattern characteristic of a plume of high chl-a water being transported down the coast. Along all transects the highest chlorophyll-a concentrations occurred inshore and decreased in the offshore direction (Fig. 4). Sub-surface peaks of chlorophyll-a were visible in transect 2 at a depth of 7-9m (Fig. 4a, 4b). Along transect 5 a single peak was located inshore along the coast (Fig. 4c). The chl-a pattern on the shelf during this cruise is consistent with a low density plume overlying more dense water on the shelf.

Based on the cross-shelf pattern of chl-a in surface waters, three broad zones were identified. The first is a shelf zone that is delineated by chl-a concentrations <0.5 μg l. This zone extends offshore and south of the baymouth. The second zone that can be identified is a high chl-a plume zone. This plume zone is confined to the coast south of the

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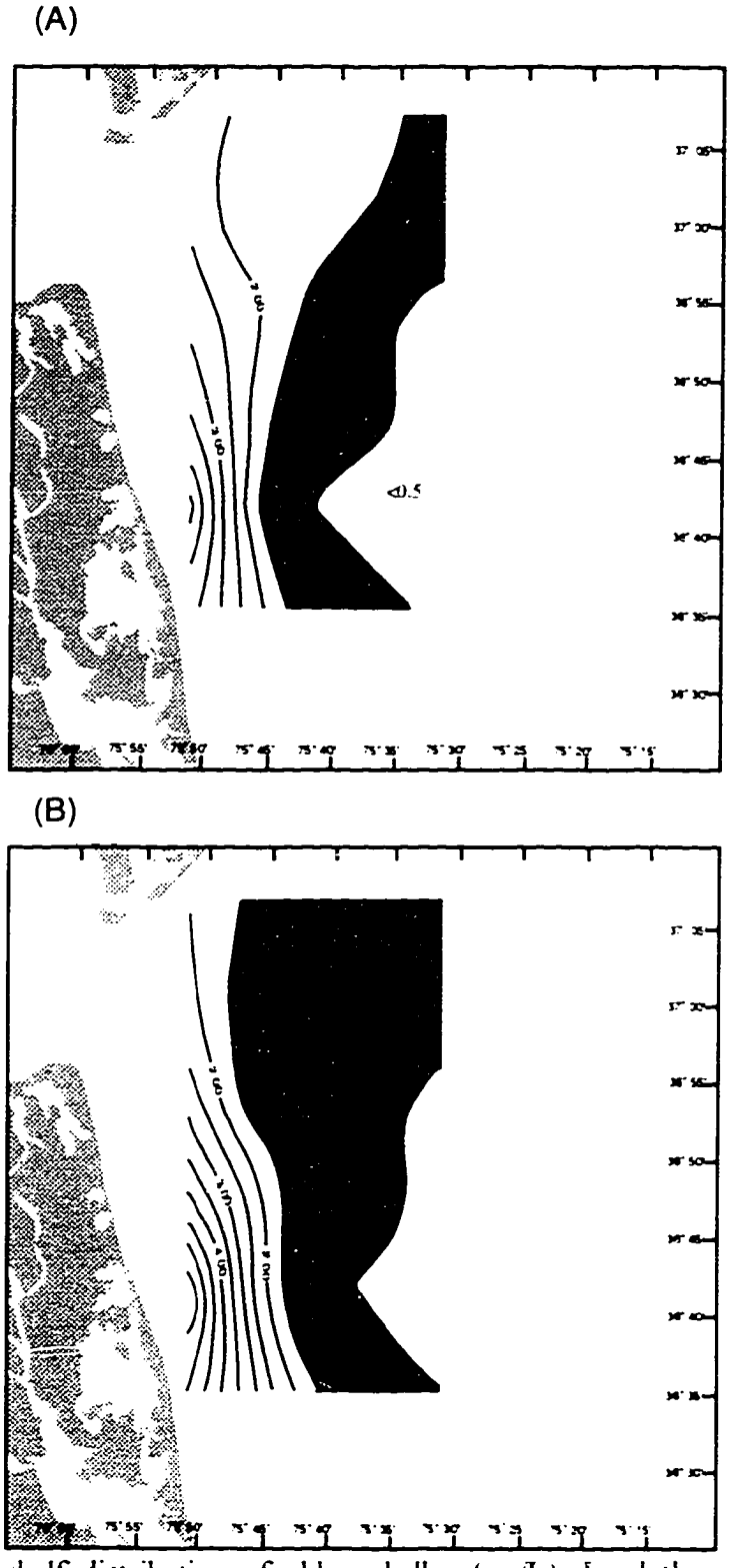

Figure 3. Cross-shelf distribution of chlorophyll-a (μg/L). Isopleths are marked at 0.5 μg/L increments and hatched area encompasses frontal zone delineated by chlorophyll-a concentrations >0.5 μg/L -1.5μg/L. (A) 1 meter, (B) 5 meters

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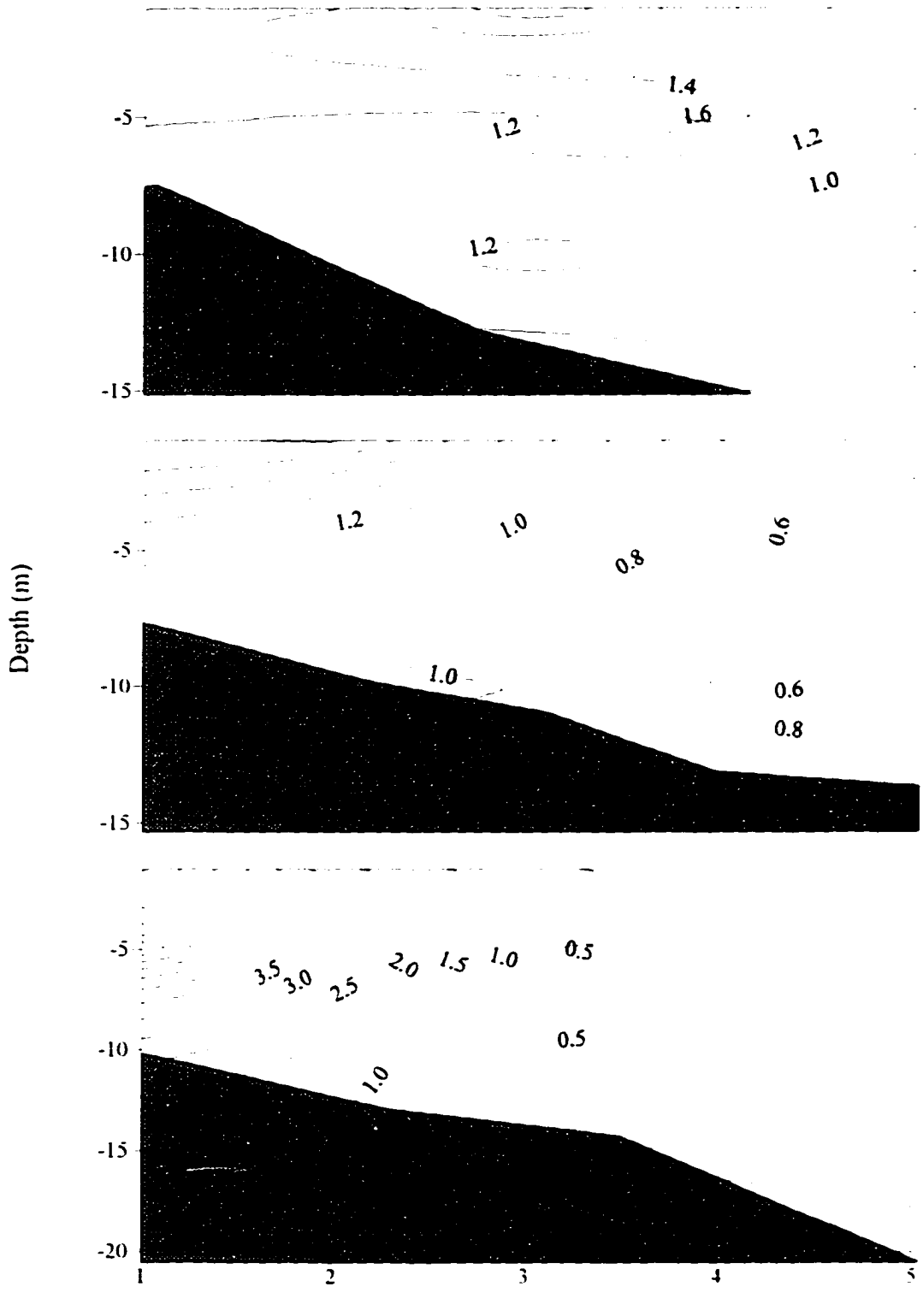

Figure 4. Distribution of chlorophyll-a (μg/L) along three transects during the period July 26 - 29, 1992. (A) Distribution along transect 2 offshore of the Chesapeake Bay mouth. (B) distribution along transect 3 off of Cape Henry, (C) distribution along transect 5 off of Virginia Beach, South of the Chesapeake Bay Mouth

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baymouth and was defined by chl-a concentrations >1.5 µg/L. The final area comprised intermediate chl-a concentrations (>0.5 and <1.5 µg/L) and will be considered the mixed or frontal zone.

Ichthyoplankton Density and Composition

Distinctly different taxonomic groupings were observed between the three zones (plume, frontal and shelf). In plume waters 23 taxa were collected. Six of these taxa occurred at densities >1.0/100m^3, including the estuarine-spawned taxa *Anchoa* spp., *Symphurus* spp., and Sciaenidae (Table 2). *Anchoa* spp. exhibited the highest mean density (89/100m^3), while shelf taxa were present, but rare. *Etropus microstomus* and *Prionotus* spp. were the most common shelf taxa, but densities of these larvae were <0.5/100m^3.

Within the frontal zone (Table 2) 27 taxa were identified. Ten taxa occurred at densities >1.0/100m^3. *Anchoa* spp. were the most abundant taxa collected within the frontal zone (25/100m^3). Two shelf taxa, *Etropus microstomus* and *Centropristis striata*, ranked second and third in abundance (14/100m^3 and 5/100m^3, respectively). Other offshore or expatriate taxa were captured in low numbers within this zone including *Xyrichtys novacula* and *Anguilla* leptocephali.

Within the shelf waters, ten taxa occurred at mean densities >1.0/100m^3 (Table 2). The three most abundant taxa were *Etropus microstomus*, *Centropristis striata*, and *Prionotus* spp. Only two of the most common taxa were from the plume and exhibited low mean abundances. These plume taxa were *Anchoa* spp. (2/100m^3) and *Symphurus* spp. (3/100m^3). Many more shelf, expatriate and offshore taxa were captured in the shelf zone including *Xyrichtys novacula* and *Bothus* spp. and *Anguilla* leptocephali.

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Table 2. Mean density of ichthyoplankton (#/100m^3) within plume (n=38), frontal (n=35) and shelf (n=24) zones of the inner continental shelf, July 26-29, 1992.

	PLUME			FRONTAL			SHELF		
Variable	Mean	Std. Deviation	Maximum	Mean	Std. Deviation	Maximum	Mean	Std. Deviation	Maximum
Anchoa spp.	89.84	180.72	767.45	25.33	53.47	285.86	2.58	5.17	20.59
Angulla leptocephalus	0.00	0.00	0.00	0.01	0.05	0.27	0.01	0.05	0.24
Astroscopus guttatus	0.09	0.25	0.88	0.45	0.67	2.73	0.57	0.80	2.63
Atherinidae	0.02	0.09	0.60	0.00	0.00	0.00	0.00	0.00	0.00
Blenniidae 1	1.05	2.36	12.20	2.69	3.61	14.24	1.70	3.20	14.91
Bothus spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.31	1.51
Carangidae 1	0.00	0.00	0.00	0.01	0.04	0.23	0.12	0.26	1.09
Centropristis striata	0.07	0.20	0.87	5.57	6.91	26.49	7.11	10.49	44.92
Citharichthys arctifrons	0.02	0.14	0.87	0.14	0.29	1.32	0.06	0.17	0.71
Cynoscion nebulosus	0.05	0.20	1.20	0.10	0.37	2.10	0.09	0.40	1.98
Etropus microstomus	0.28	0.56	2.19	14.58	25.09	107.01	10.08	14.00	58.77
Glyptocephalus spp	0.00	0.00	0.00	0.01	0.04	0.24	0.00	0.00	0.00
Gobiosox strumosus	0.66	1.95	9.81	0.17	0.66	3.23	0.01	0.08	0.40
Gobiidae	0.15	0.50	2.87	0.32	0.61	2.42	0.32	0.60	2.13
Hippocampus spp	0.02	0.14	0.88	0.00	0.00	0.00	0.01	0.05	0.27
Menticirrhus spp	4.54	7.05	30.59	4.80	5.77	22.65	1.89	2.64	9.09
Monacanthidae	0.00	0.00	0.00	0.01	0.04	0.22	0.02	0.08	0.35
Monolene spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.22
Ophidion spp	0.07	0.19	0.87	1.61	1.46	5.56	1.68	2.22	7.32
Peprilus triacanthus	0.06	0.18	0.95	2.37	3.04	13.53	1.72	2.50	10.20
Pleuronectidae	0.01	0.05	0.33	0.18	0.39	1.89	0.02	0.08	0.34
Prionotus spp	0.34	0.63	2.66	3.78	3.69	14.66	3.37	5.62	21.53
Rachycentridae	0.03	0.15	0.95	0.00	0.00	0.00	0.00	0.00	0.00
Sciaenidae 1	10.35	21.09	106.21	4.13	9.34	38.83	0.41	1.75	8.52
Scombridae 1	0.06	0.24	0.95	0.91	1.62	6.62	1.00	1.48	6.39
Symphurus spp.	18.49	60.58	365.08	5.45	7.98	34.17	2.99	3.73	13.49

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Table 2 continued

	PLUME			FRONTAL			SHELF		
	Mean	Std. Deviation	Maximum	Mean	Std. Deviation	Maximum	Mean	Std. Deviation	Maximum
Syngnathus fuscus	0.02	0.14	0.88	0.02	0.16	0.94	0.04	0.18	0.90
Synodus foetens	0.00	0.00	0.00	0.20	0.51	2.67	0.35	0.93	4.57
Tetraodontidae	0.01	0.06	0.39	0.02	0.79	0.37	0.00	0.00	0.00
Trinectes maculatus	1.89	8.47	51.67	0.03	0.18	1.07	0.00	0.00	0.00
Unknown #1	0.00	0.00	0.00	0.03	0.15	0.87	0.01	0.04	0.24
Xyrichtys novacula	0.00	0.00	0.00	0.03	0.09	0.33	0.09	0.19	0.83

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Table 3. Factor loadings for fourteen taxa used to derive assemblages in PCA for daytime and nighttime during July 26-30, 1992. Factor loadings >0.5 were used to derive assemblage membership during the daytime samples. At night assemblages were not clearly described by this cutoff value.

	Daytime			Nighttime		
Species	**Factor 1**	**Factor 2**	**Factor 3**	**Factor 1**	**Factor 2**	**Factor 3**
Anchoa spp	-0.197595	0.868239	0.220259	-0.141974	-0.561681	0.064172
Symphurus spp	0.214855	0.856879	0.026652	-0.235314	-0.464664	0.006613
Prionotus spp	0.705958	0.278468	-0.354102	-0.378435	0.093079	-0.127026
Astroscopus guttatus	0.698533	-0.15839	-0.292798	-0.252969	0.018583	0.081999
Synodus spp	0.35957	0.008119	-0.643789	-0.179589	0.093384	-0.154273
Centropristis striata	0.885225	-0.215111	0.248467	-0.381753	0.230794	-0.076417
Ophidion spp	0.782295	-0.201954	0.261974	-0.342584	0.109339	-0.152544
Menticirrhus spp	0.562657	0.681615	0.148575	-0.223051	-0.509413	0.035778
Etropus microstomus	0.856516	-0.287468	0.100132	-0.360558	0.293143	-0.060029
Citharichthys arctifrons	0.451705	-0.133447	0.432718	-0.125828	-0.102983	-0.757006
Scombridae	0.642041	0.314605	-0.30924	-0.240361	0.043616	0.491757
Peprilus triacanthus	0.901316	-0.060284	0.064968	-0.336213	0.126814	0.313085
Gobiidae	0.213741	0.104465	0.34653	-0.235615	-0.10783	0.047755

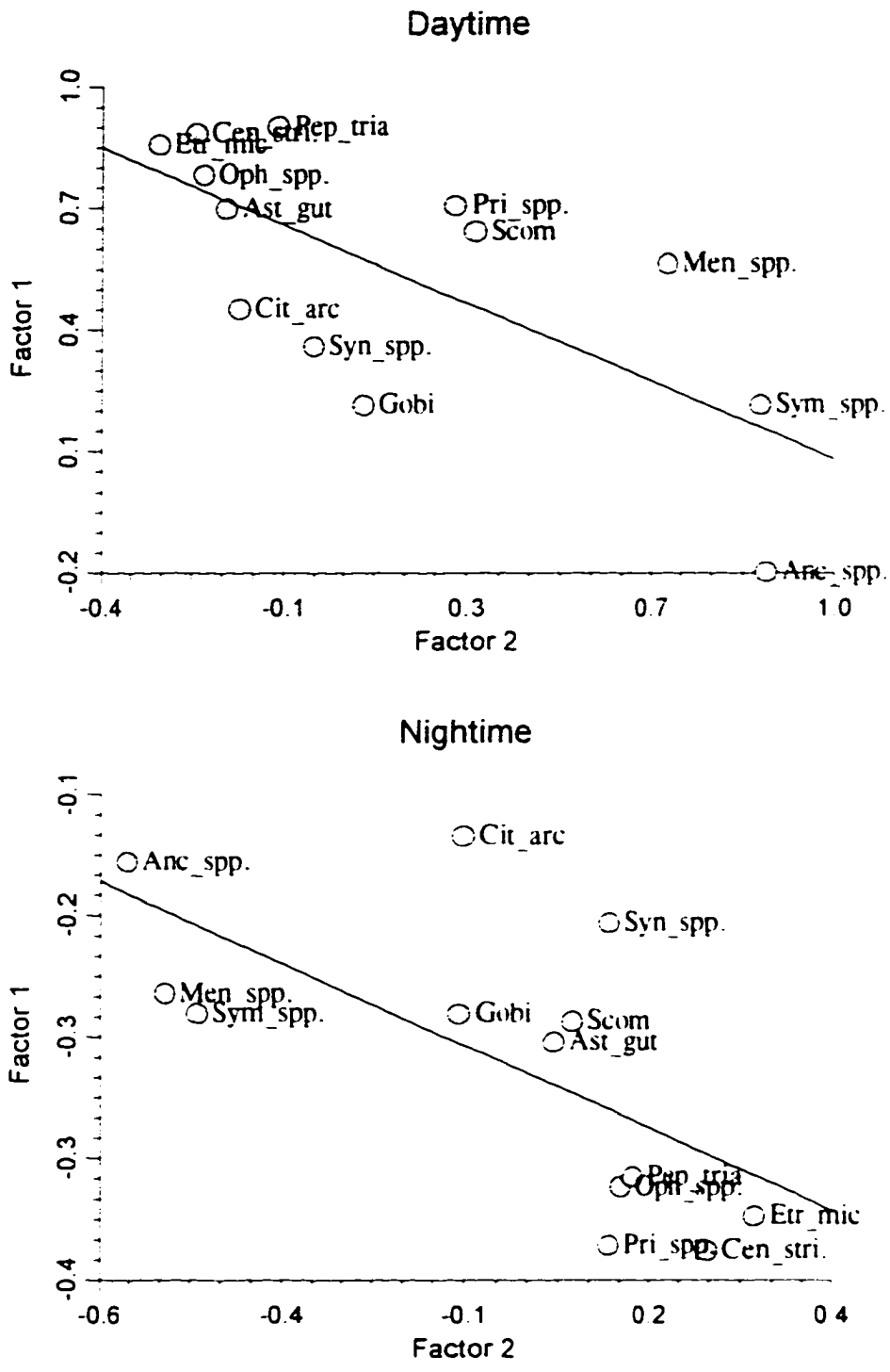

Figure 5 Factor loadings plots of day-time (a) and night-time (b) PCA results The lines are regression lines that are significant <0 01 The two end-members of these ordinations represent the plume and the shelf assemblage, and indicators of these assemblages are *Anchoa* spp (the plume), and *Etropus microstomus* (the shelf)

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PCA revealed two distinct assemblages of larvae based on loadings of the first two factors. The first two factors accounted for 57% of the variance within the data matrix for both daytime and nighttime analyses (Table 3). Regressions of the first two factor loadings for both the daytime (r^2=0.4860, p <0.004) and nighttime (r^2=0.4274, p<0.02) PCAs were significant. This non-random distribution of factor scores indicates that the derived assemblages are real. In both cases, Factor 1 loadings were associated with *Etropus microstomus*, *Prionotus* spp., *Centropristis striata*, *Ophidion* spp., and *Peprilus triacanthus*. Factor 2 loadings were always associated with *Anchoa* spp., *Symphurus* spp. and *Menticirrhus* spp.

Factor loadings for the remaining five taxa (Gobiidae, Scombridae, *Astroscopus guttatus*, *Synodus* spp., and *Citharichthys arctifrons*) did not show a consistent affinity for either the plume or shelf assemblage. This is reflected in inconsistent factor scores between day and night (Fig. 5). This suggests that larval assemblages may become less defined at night. Based on the results of this PCA and the criteria defined in chapter 1, *Anchoa* spp. and *E. microstomus* were selected as indicator taxa for the plume and the shelf assemblages, respectively.

Species-specific differences among zones

Differences were found in the distributions of the three taxa examined in this study. The two indicator taxa, *Anchoa* spp., and *E. microstomus*, were retained within their water masses, but exhibited distinctly different distributions between zone, sample depth and time of day.

Anchoa spp. densities were consistently higher within the plume and frontal zones both day and night (Table 4). Further, there was no increased larval abundance within the

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frontal zone that would indicate that *Anchoa* spp was aggregated within this area (Table 4). These results indicate that *Anchoa* spp. larvae were retained within the high chl-a waters at all times (Fig. 6)

Larval *E. microstomus* were most abundant within the frontal and shelf waters Overall, *E. microstomus* was more abundant at night than during the day, and this suggests that net avoidance may occur during the day The results of the ANOVA also showed that *E. microstomus* was more abundant at depth (7-9m) during the day (Table 5), and were distributed throughout the water column at night (Fig 7) A significant (time of day - zone) interaction was found complicating interpretation of these factors (Table 5)

Ontogenetic changes in assemblage membership

Symphurus spp larvae did not show any significant difference between zone, sample depth or time of day based on a three-way ANOVA (Table 6) This suggests that, unlike *Anchoa* spp., *Symphurus* spp., was not effectively retained within the high chl-a water representing the plume (Table 6) This was unexpected since the pattern of mean larval density is similar to that observed for *Anchoa* spp., especially at night (Fig 8)

The cross-shelf distribution of ontogenetic stages of both *Anchoa* spp and *E. microstomus* did not vary greatly Each taxa was retained within the plume or shelf water masses, respectively In contrast, the mean length of *Symphurus* spp., increased with distance from shore (Fig 9 a, b) The distribution of the smaller *Symphurus* spp larvae (< 3.5 mm) was similar to the overall pattern of *Symphurus* spp abundance (Fig 7 a, b) Larger larvae (>3.5 mm) however, exhibited a spatial pattern that differed from either indicator taxa and from the overall larval abundance of *Symphurus* spp These larger

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Table 4. Three-way analysis of variance of rank transformed density of *Anchoa* spp. Main effects are zone (plume, frontal or shelf), sample depth (1m, 3m, 7m, 9m), time of day (day or night) and three testable two way interactions * Term significant at alpha = 0.05.

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level
A (SAMPLE DEPTH)	3	15167.43	5055.81	9.85	0.000016*
B (TIME OF DAY)	1	0.9387837	0.9387837	0.00	0.966005
AB	3	2411.398	803.7995	1.57	0.204945
C (ZONE)	2	8998.545	4499.272	8.77	0.000387*
AC	6	2135.208	355.868	0.69	0.655723
BC	2	79.64176	39.82088	0.08	0.925431
ABC	6	1974.527	329.0878	0.64	0.696947
S	73	37470.97	513.301		
Total (Adjusted)	96	75563.5			
Total	97				

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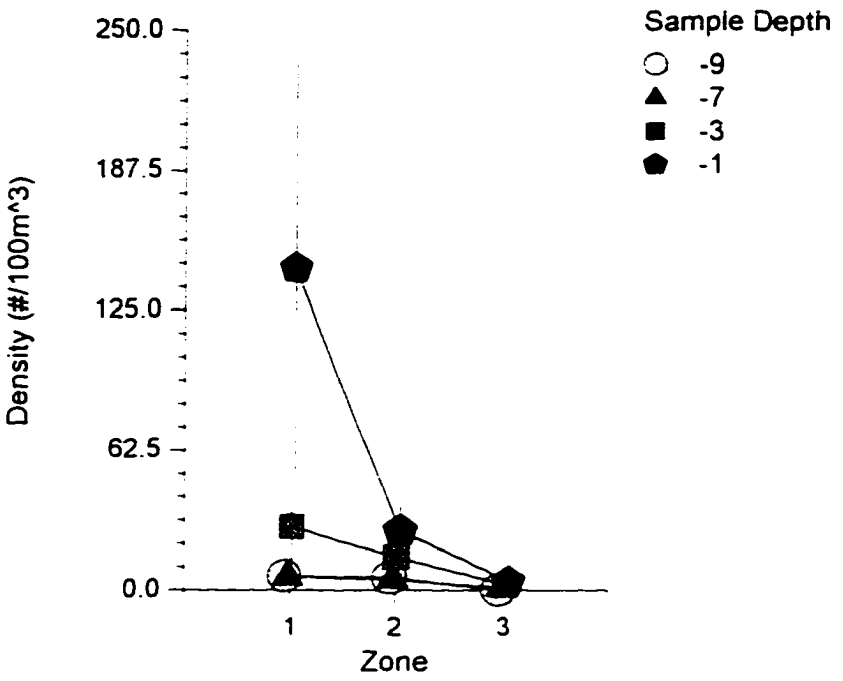
(A) Overall *Anchoa* spp - Daytime



(B) Overall *Anchoa* spp - Nighttime

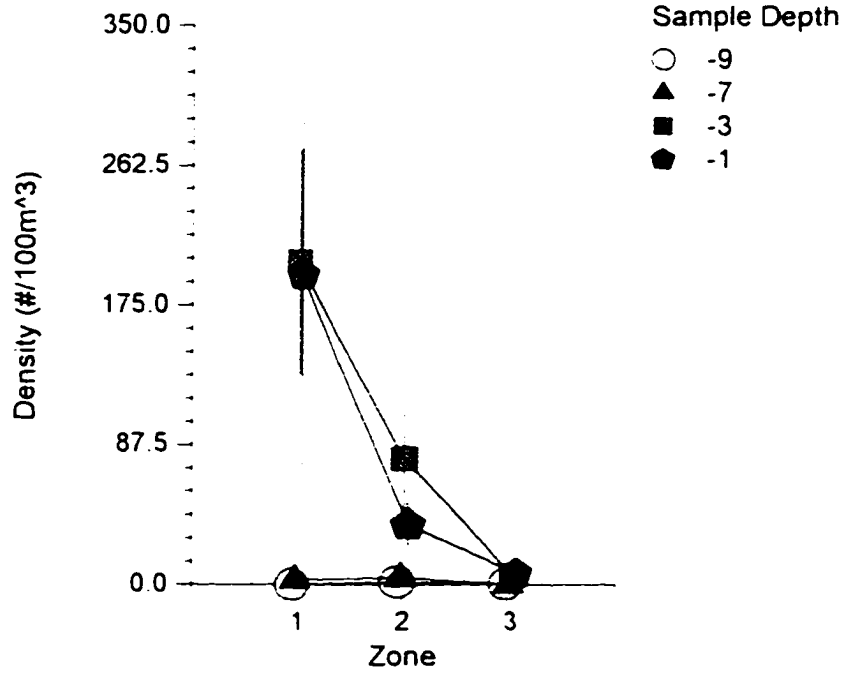


Figure 6. Density of *Anchoa* spp in all three zones (plume, frontal and shelf) during daytime (A) and nighttime (B) (error bars are ±1 SE)

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Table 5. Three-way analysis of variance of rank transformed data for *Etropus microstomus* density. Main effects are zone (plume, frontal or shelf), sample depth (1m, 3m, 7, 9m), time of day (day or night) and three testable two way interactions. * Term significant at alpha = 0.05

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level
A (SAMPLE DEPTH)	3	2222.85	740.9498	3.02	0.035015*
B (TIME OF DAY)	1	3174.537	3174.537	12.95	0.000579*
AB	3	1871.549	623.8497	2.55	0.062611
C (ZONE)	2	23621.29	11810.65	48.19	0.000000*
AC	6	841.4182	140.2364	0.57	0.751223
BC	2	4519.62	2259.81	9.22	0.000269*
ABC	6	2302.3	383.7166	1.57	0.169479
S	73	17892.58	245.1039		
Total (Adjusted)	96	73800.5			
Total	97				

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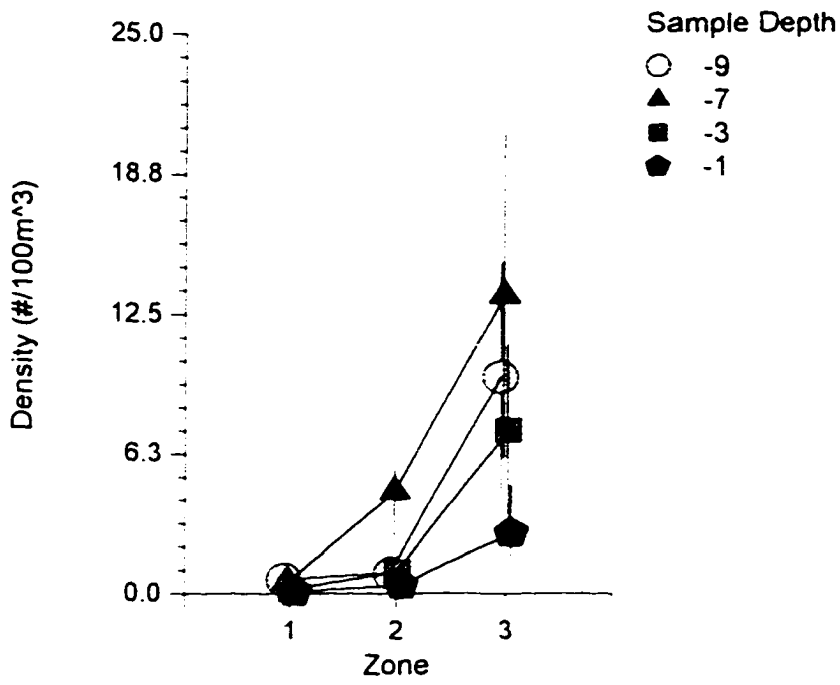
(A) Overall *Etropus microstomus* - Daytime



(B) Overall *Etropus microstomus* - Nighttime

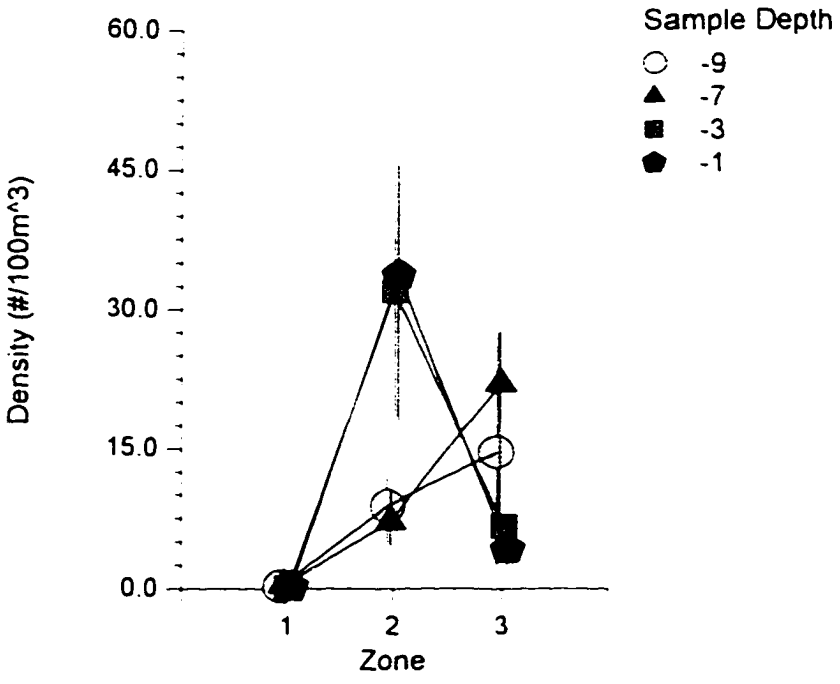


Figure 7. Density of *Etropus microstomus* in all three zones (plume, frontal and shelf) during daytime (A) and nighttime (B) (error bars are ±1 SE)

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Table 6. Three-way analysis of variance of rank transformed density of *Symphurus* spp. Main effects are zone (plume, frontal or shelf), sample depth (1m, 3m, 7m, 9m), time of day (day or night), and three testable two way interactions. * Term significant at alpha = 0.05*

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level
A (SAMPLE DEPTH)	3	2130.643	710.2144	0.87	0.460595
B (TIME OF DAY)	1	81.42598	81.42598	0.10	0.753013
AB	3	3653.454	1217.818	1.49	0.223822
C (ZONE)	2	1807.05	903.5251	1.11	0.336027
AC	6	2274.319	379.0531	0.46	0.832445
BC	2	53.75532	26.87766	0.03	0.967620
ABC	6	4447.838	741.3063	0.91	0.493916
S	73	59581.01	816.1782		
Total (Adjusted)	96	75478			
Total	97				

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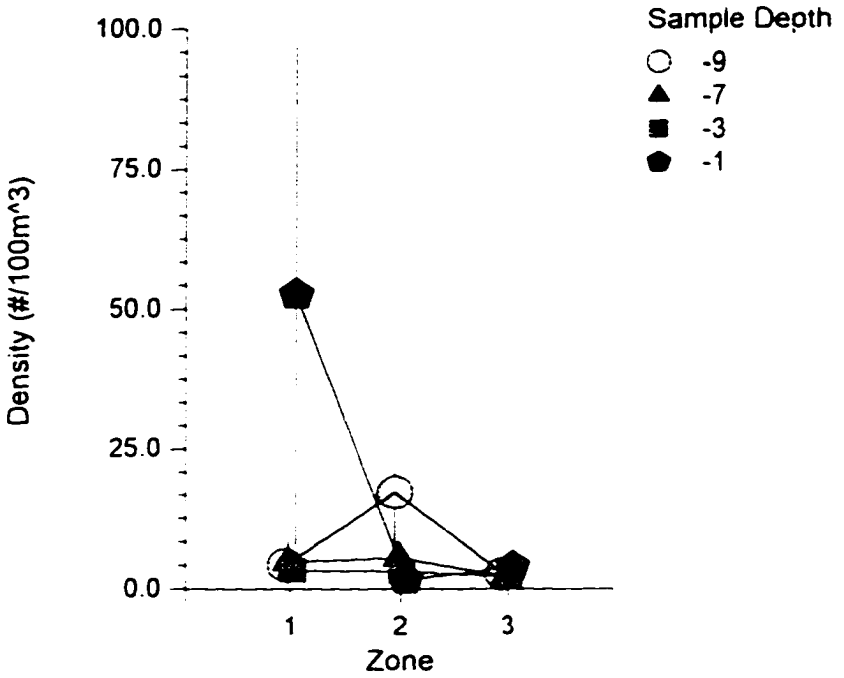
(A) Overall *Symphurus* spp. - Daytime



(B) Overall *Symphurus* spp - Nighttime

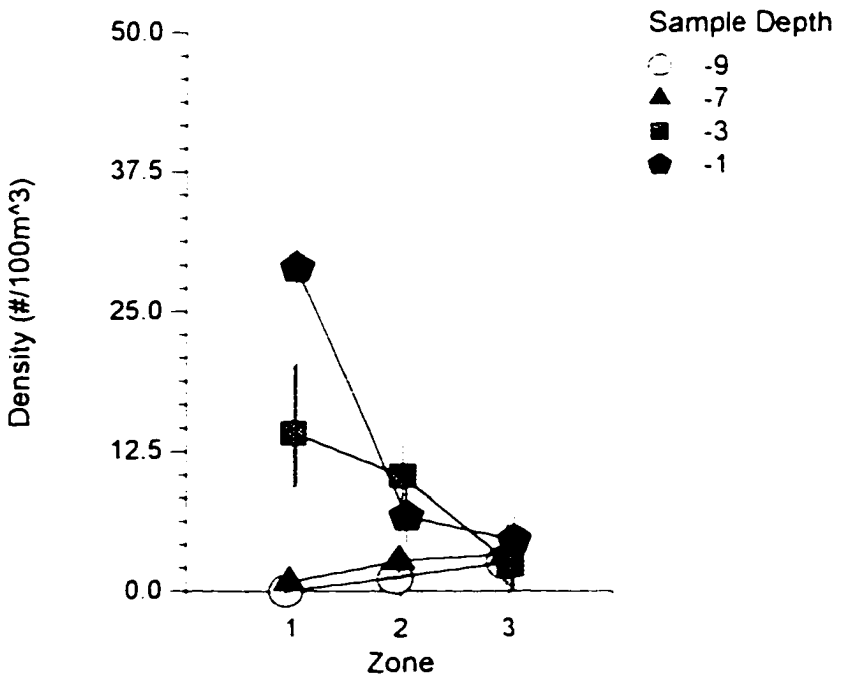


Figure 8 Density of *Symphurus* spp in all three zones (plume, frontal and shelf) during daytime (A) and nighttime (B) (error bars are ±1 SE)

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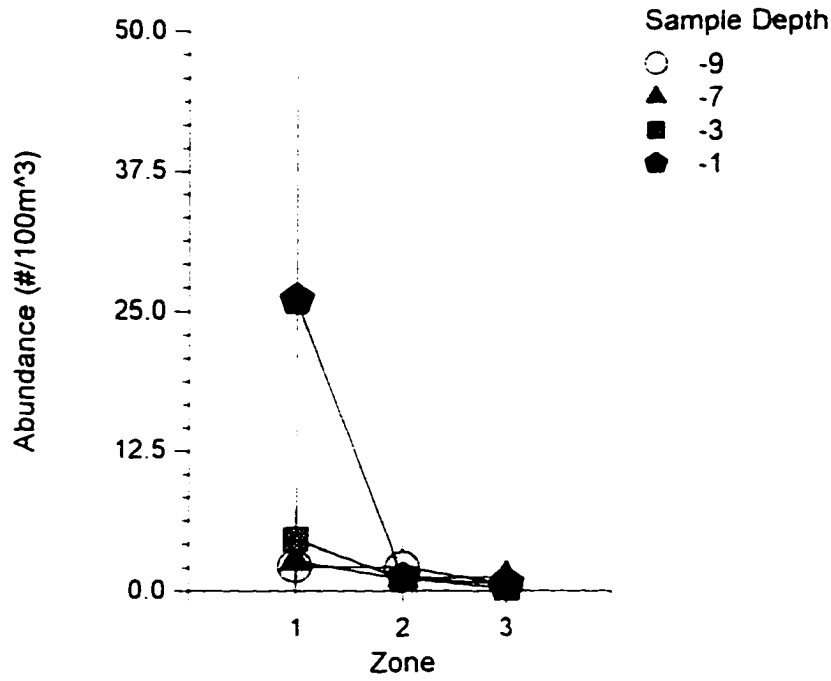
(A) Distribution of *Symphurus* spp (<3 5 mm)



(B) Distribution of *Symphurus* spp (> 3 5 mm)

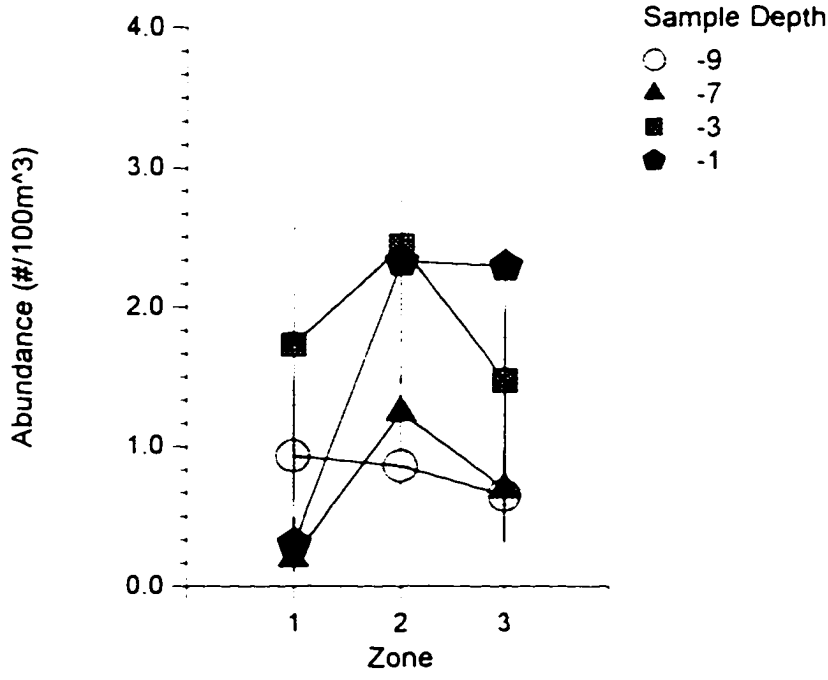


Figure 9 Abundance of ontogenetic stages at each depth and zone for *Symphurus* spp (a) Abundance of small (<3 5 mm) *Symphurus* spp reflects a cross shelf pattern that is similar to the plume indicator, *Anchoa* spp , (b) Abundance of large (> 3 5 mm) *Symphurus* spp does not reflect retention within the plume suggesting that this taxa undergoes an ontogenetic migration from the plume to the shelf

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larvae were increasingly more abundant across the shelf, suggesting that this taxa may undergo an ontogenetic migration from the plume to the shelf.

Discussion

The cross-shelf distribution of chlorophyll-a was consistent with patterns observed in other studies in the Chesapeake Bay region (Rutledge 1982, Boicourt *et al.* 1987, Olney 1996, Reiss and McConaugha 1997 in prep.) Both Rutledge (1982) and Boicourt *et al* (1987) found that cross-shelf sections of chl-a closely followed salinity distribution, and during summer chl-a concentrations decreased rapidly across the 30 psu isohaline. In this study, there was no increased chl-a concentrations within the frontal zone that would suggest aggregation of biomass or increased productivity. Instead, the frontal zone was an area of intermediate chl-a concentrations. Studies have found broad frontal zones with increased chl-a concentrations associated with river plumes that empty onto continental shelves (Ortner *et al.* 1983, Sabates 1990, Grimes and Finucane 1991, Sabates and Olivar 1995). The patterns in chl-a concentrations during this study however, are consistent with a plume of chl-a rich water traveling down the coast that is separate from the surrounding shelf waters. This consistency indicates that cross-shelf chl-a distributions observed herein adequately reflect the position of the Chesapeake Bay outflow plume, and the inner-shelf waters.

The cross-shelf distributions of the indicator taxa, *Anchoa* spp. and *E. microstomus* indicate that the two assemblages derived during this study were delineated by the Chesapeake plume. The assemblages derived in this study differed from the plume and shelf assemblages derived by Olney (1996) in two ways. During the current study no *M. undulatus* were found, while Olney (1996) found large numbers of *M. undulatus*

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present on the shelf. This difference can be attributed to the timing of the two studies. Samples during this study were collected prior to the spawning season, whereas Olney's study followed it. Second, during the current study *Symphurus* spp. were found to be associated with the plume assemblage. This differs with the findings of Olney (1996) who classified *Symphurus* spp. with the shelf assemblage. The consistency of the findings of the two studies indicates that the general organization of larval fish assemblages within the inner-shelf is consistent over time, although membership may vary based on the spawning cycles of some taxa.

During this study, ichthyoplankton were not concentrated within the frontal zone. This differs with findings that ichthyoplankton are aggregated in broad frontal zones resulting from continuous formation and re-formation of the front on a broad scale (Pingree 1974; Grimes and Finucane 1991, Kingsford 1990). Olney (1996) found that larval abundance was not increased in the "mixed water" between plume and shelf assemblages in the Chesapeake Bay plume. He suggested that the intermediate densities of ichthyoplankton in the "mixed water" were related to mixing of plume and shelf assemblages. Reiss (chap. 3) however, found that the Chesapeake Bay plume front effectively delineated the seaward extent of the plume assemblage under a variety of conditions. Therefore, the intermediate larval densities within the frontal zone during this study and Olney (1996), arise from sampling designs that did not sample the plume front as a distinct feature. Aggregation may be scale dependent, i.e. if samples were obtained closer to the front, or if the front were better delineated, increased larval abundances inside and outside of the front might have been observed.

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The manner in which the Chesapeake Bay outflow plume affected the distribution of taxa varied during this study *Etropus microstomus* exhibited a significant diel change in vertical distribution that may indicate a migration to depth during the day Retention in shelf waters against the net sub-surface estuarine inflow could result from migration into surface waters at night where the net flow is offshore, and then migrating to a depth where the water flow is minimal during the daytime On the Virginia shelf, the pycnocline occurs at depths between 5 and 15 m depending on the distance from the shore (Reiss chap 3, and chap 5, Olney 1996; Boicourt *et al* 1987) Although no samples were collected deeper than 9m in this study, the position of maximal abundance of this taxa during the day, (7-9 m), may have been associated with the pycnocline A similar change in vertical distribution for *E. microstomus* has been found on the shelf by Cho (1996) He found *E. microstomus* concentrated at the depth of the pycnocline (~15 m) during the day, and were found in surface waters at night He hypothesized that this was a mechanism that resulted in retention of these larvae on the mid-shelf

Many studies have found that larval fish exhibit diel or semi-diel differences in vertical distributions (Smith *et al* 1978, Kendall *et al* 1984) These changes have been perceived as adaptive, resulting in increased retention or selective transport (Weinstein *et al* 1980, Stephenson and Powers 1988), although this hypothesis is the source of some debate (Neilson and Perry 1989; Sclafani *et al* 1993) There are, however, other factors that may create the appearance of a vertical migration including, differential catchability of larvae between day and night and movement of water masses over one another In order to determine whether the diel changes in vertical distribution are real (i e behavioral) it is important to adequately sample the physical environment to ensure that

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vertical differences do not result from the movement of water masses over each other

The cross-shelf distribution of *Symphurus* spp. differed from that of *Anchoa* spp., suggesting that not all members of the same assemblage are affected by the physics in the same manner. Small (<3.5 mm) *Symphurus* spp. larvae were found almost exclusively within the plume, and their pattern was similar to that of *Anchoa* spp. Larger *Symphurus* spp. larvae however, were mostly found in frontal and shelf waters. The ontogenetic pattern observed here shows a cross-shelf separation of ontogenetic stages suggesting that *Symphurus* spp. switches from the plume assemblage to the shelf assemblage through ontogeny. This ontogenetic pattern may explain the apparent discrepancy between two studies of Olney (1976, 1996). Olney (1976) concluded that *Symphurus* spp., were spawned in Chesapeake Bay. However, he found that *Symphurus* spp. were ordinated with the shelf assemblage in another study Olney 1996). He suggested that this was the result of broad-scale spawning within the bay and on the shelf. The ontogenetic patterns presented here suggest an explanation for this discrepancy.

The ontogenetic pattern may simply reflect spawning preferences of the adults, but may also reflect an adaptation to maximize survival of early stage larvae. The higher chl-a (food) and stable conditions within the plume may afford an energetic benefit or may reduce predation risk to young *Symphurus* spp. in the Chesapeake Bay Plume, while the ontogenetic migration may be necessary to successfully recruit to nearshore coastal habitats (Fortier and Leggett 1982). This result however, should be considered preliminary because several species of *Symphurus* spp. are found in shelf waters and this may confuse the patterns observed for late stage larvae.

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In summary, the hypothesized vertical migration by *Etropus microstomus* may enhance retention in shelf waters and minimize transport into the Chesapeake Bay mouth in sub-surface estuarine flows. The patterns exhibited by *Symphurus* spp suggest that a switch in assemblage membership from the plume to the shelf may occur with ontogeny The differing distributions of ichthyoplankton taxa and their assemblages suggests that both physical and biological mechanisms are responsible for the maintenance of distinct ichthyoplankton assemblages in these coastal waters

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CHAPTER 3

Temporal distribution of ichthyoplankton across surface waters of the Chesapeake Bay Plume

Introduction

Riverine and estuarine plumes are dynamic and ephemeral coastal features that exhibit considerable variability in position and strength (Garvine 1974, Bowman and Esaias 1978; Boicourt 1981; Boicourt *et al.* 1987). Because of this variability, plume fronts are considered important to ichthyoplankton distribution and survival in coastal waters (Kingsford *et al.* 1986, Kingsford and Suthers 1991, Kingsford 1994). Studies have shown that movement of the leading edge of the front or of frontal zones was a primary influence on the distribution of ichthyoplankton assemblages, as well as the mesoscale spatial heterogeneity and survival of some types of fish larvae (Richardson *et al.* 1977; Govoni *et al.* 1989; Sabates 1990, Govoni and Grimes 1992, Thorrold and McKinnon 1995). By structuring and delimiting ichthyoplankton assemblages, fronts increase the patchiness of larvae and other planktonic organisms. This patchiness can effect larval survival by modifying feeding and predator-prey interactions (Wiebe 1970).

Increased primary and secondary production has been associated with frontal zones of various kinds (Pingree 1974, 1986, Kiorboe *et al.* 1988, Lohrenz *et al.* 1990, Grimes and Finucane 1991, Munk 1993). Many of these studies have also found increased abundances of larval fish at frontal zones compared to either side. Increased larval

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abundances within frontal zones have been explained by physical aggregation (Govoni *et al.* 1989; Thorrold and MacKinnon 1995), larval behavior (Kingsford and Choat 1986, Kingsford 1990; Kingsford and Suthers 1994), physics and behavior (Govoni and Grimes 1992), and adult spawning locations (Iles and Sinclair 1982; Iwatsuki *et al* 1989)

Observed increases in primary and secondary production and larval fish abundances around frontal zones have led to several hypotheses regarding the role of frontal zones to the survival and recruitment of ichthyoplankton. Iles and Sinclair (1982) argued that retention of larvae spawned within higher productivity mixed waters separated by tidal fronts would increase larval survival by minimizing advective loss Grimes and Finucane (1991) hypothesized that frontal aggregation, regardless of the mechanism, would lead to above average food concentrations, higher growth rates, and higher survival despite the potential for increased mortality from predators

Plume fronts occur between the offshore spawning location and juvenile nursery areas (estuaries) of shelf-spawned, estuarine-dependent larval species, making fronts potentially important regulators in the recruitment pathway of larvae (Shaw *et al* 1985) Some researchers have hypothesized that frontal zones may act as staging areas for recruitment to juvenile habitats, by concentrating larvae at the mouths of inlets or offshore of reefs (Kingsford 1990) Others hypothesized that transport along fronts was an important recruitment pathway for shelf-spawned estuarine-dependent ichthyoplankton (Shaw *et al* 1985; Iwatsuki *et al* 1989; Nakata 1989)

Increased growth rates of larval fish have been demonstrated at frontal zones in the North Sea (Kiorboe *et al* 1988, Munk 1993), while studies on larval growth in the vicinity of the Mississippi River Plume front were inconclusive (Powell *et al.* 1990) These

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results suggest that not all frontal zones are comparable or act in the same manner

Studies on the temporal stability of larval assemblages across frontal zones have shown them to recur seasonally based on yearly spawning patterns of adults (Richardson and Pearcy 1977). Within seasons, some taxa may switch between assemblages Oceanographic variability has been invoked to explain the changes in assemblage membership (Cowen *et al.* 1993; Sabates and Olivar 1995). Understanding the temporal variability of mesoscale and fine-scale features like plume fronts should reveal how physical mechanisms may influence survival and recruitment of ichthyoplankton taxa

The mesoscale spatial (<10 km) and temporal (bi-weekly) distribution of larval fish in surface waters across the Chesapeake Bay plume front was studied to determine how the plume structures ichthyoplankton assemblages and how the structure varies intra-seasonally. Previous studies within the Chesapeake Bay mouth have classified invertebrate and vertebrate larvae based on hydrographic properties of the water where they were collected (temperature and salinity), but did not sample the plume front as a distinct feature (Seibel 1993; Olney 1996). These studies were not able to determine whether the larval assemblages were maintained by physical mechanisms or simply reflected mixing of water masses between plume and shelf waters. The importance of spatial pattern and integrity of ichthyoplankton assemblages in relation to variability in the physical environment may be elucidated by examining cross-frontal ichthyoplankton distributions within a season. This information is critical in evaluating the importance of estuarine plume fronts and mesoscale oceanographic features on recruitment and survival of ichthyoplankton taxa.

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Oceanographic Setting

The oceanography of the Virginia shelf is characterized by two principal water masses: Mid-Atlantic Shelf water and Chesapeake Bay plume water. Mid-Atlantic Shelf water has salinities in excess of 30 psu and can range from 30-34 psu (Manning 1991). The Chesapeake Bay plume, exhibits salinities considerably less than 30 psu, and can range from less than 15 to about 25 psu in the baymouth (Boicourt 1981). Temperature varies seasonally, but during summer plume water is usually warmer (22 ^{0}C) than shelf water (10-22 ^{0}C). Mid-Atlantic Cold Pool water (~33 psu, 7-12 ^{0}C) can also occur on the inner shelf during summer in response to coastal upwelling (Hicks and Miller 1980).

The Chesapeake Bay plume exits the bay and turns south in response to the Coriolis force (to the right in the northern hemisphere), resulting in a coastally trapped current. The bathymetry of the inner shelf is simple, with few channels or other bathymetric features that can steer circulation (Boicourt 1981, Valle-Levinson 1995). The Chesapeake Bay estuarine circulation has been shown to transport sub-surface drifters into the bay from as far seaward as 50 km (Norcross and Harrison 1967) independent of estuary-shelf interaction, so it may be responsible for the transport of shelf-spawned estuarine-dependent larvae to the bay (Norcross 1983, 1991).

On the shelf, plume position and strength are modified by wind forcing, tidal conditions, and river flow (Boicourt 1981, Boicourt *et al.* 1987). The seaward edge of the outflow plume forms a front that results from the interaction of lighter baywater flowing over more dense shelf water. Separation of the two water masses is not complete, and at the front local mixing due to downwelling is intensified even while forming a boundary

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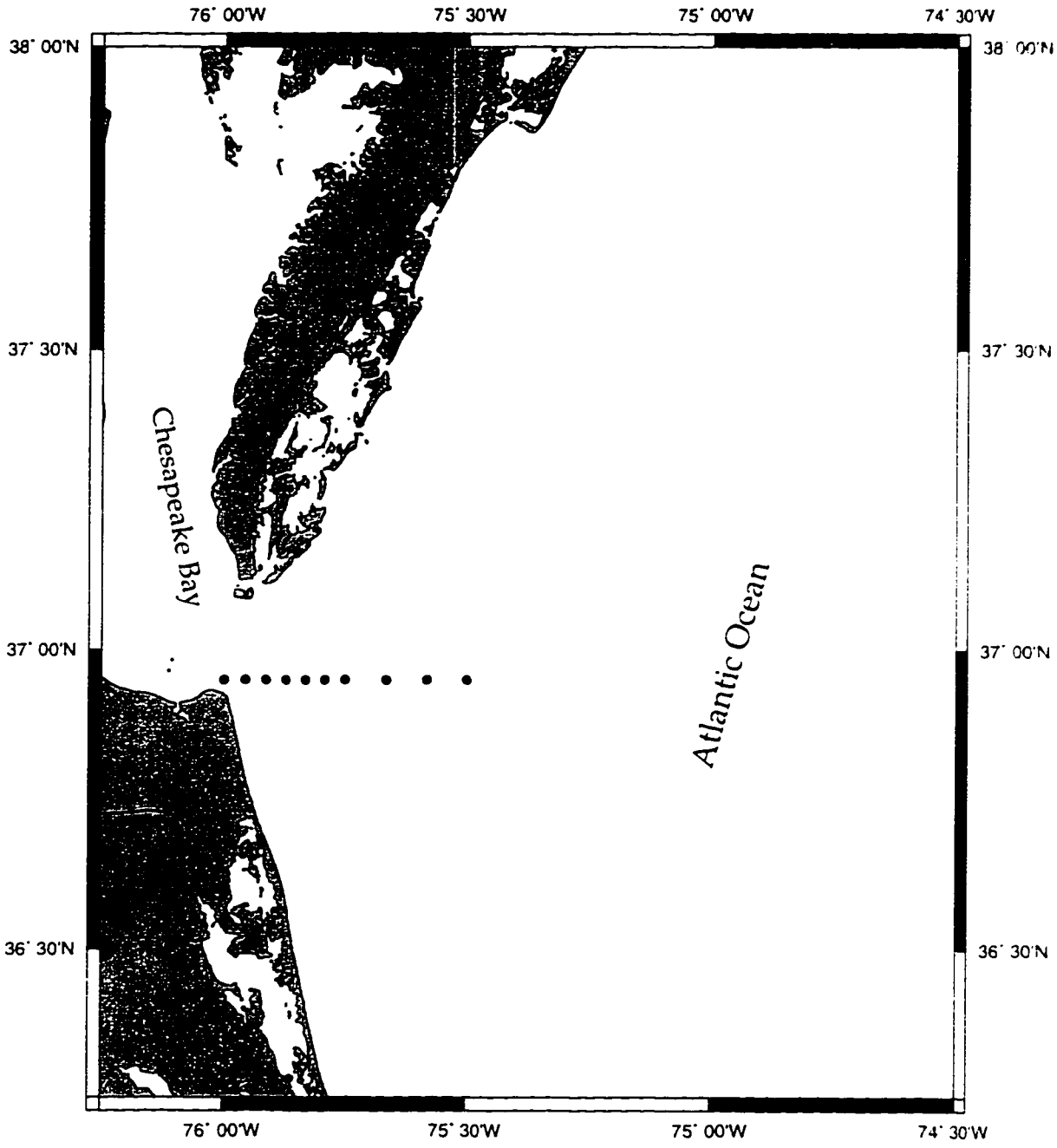

Figure 10 - Map of the Chesapeake Bay Mouth and the Inner Continental Shelf Fixed station locations (●) for the summer of 1994 are shown.

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between these two water masses (Bowman 1978). If plume dynamics can aggregate or retain larvae within the 50 km zone of estuarine influence, estuarine-dependent larvae may have an increased probability of recruitment as a result of estuarine circulation or wind driven advection.

Methods and Materials

Ichthyoplankton were sampled along a transect eastward to the baymouth, from the south side of Chesapeake Bay (Cape Henry 76° 00'W) to approximately 45 km east (75° 30'W) along latitude 36° 56'N (Fig. 10). Stations along the transect were fixed and located at 3.5 km increments for the first 15 km of the transect. Thereafter, stations were located at 7.5 km increments. Fronts were sampled when they were visually obvious (water color, flotsam). Since multiple fronts were present on the shelf at times, the 30 psu front was defined as the Chesapeake Bay plume shelf water interface (Boicourt 1981, Boicourt *et al.* 1987; Olney 1996). The transect was sampled on four occasions (July 5, August 9, September 7, September 20). On August 9, mechanical difficulties forced the shortening of the transect by one station at the end. On September 7, an extra station was added at the end of the transect.

Ichthyoplankton was collected with a $1m^2$ Tucker trawl equipped with 202μ (July 5) or 333μ (remaining cruises) Nitex mesh nets. Net size was switched to the larger mesh because the 202μ nets were easily fouled with algae and gelatinous plankton. All nets were equipped with General Oceanics mechanical flowmeters (model 2030) to quantify the volume filtered. On July 5, two replicate samples were taken at 1m. On all the remaining cruises (Aug. 9, Sept. 7, Sept. 20) single samples were taken at 1m and 3m depths (measured from the top of the tucker trawl). At frontal stations, two serial surface tows

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were made along the flotsam line. These two tows were combined and used as a single value in all analyses. All tows were five minutes in duration and ichthyoplankton densities were standardized to #/100m^3 of water filtered.

A hydrographic cast was made at each station using a Seabird Electronics model SBE-25e CTD. Conductivity, temperature and pressure were used to calculate salinity and density. Three replicate surface water samples were collected at each station for chlorophyll-a (chl-a) analysis. Chlorophyll-a samples were frozen for storage, extracted in acetone (90%) and analyzed using fluorometric techniques on a Turner Designs model-10 fluorometer (Parsons *et al.* 1984). Chl-a is used as a first order measure of potential food availability since the net mesh was too large to properly sample larval food.

Data Analysis

Hydrographic data from each transect were plotted as temperature-salinity (T-S) diagrams in order to characterize the plume and the associated water masses. Cross-shelf sections of important hydrographic variables (temperature, salinity and density) were also constructed to visualize the oceanographic regimes sampled using SURFER (Golden Software, Inc.).

Bulk stratification, the difference in density between two depths ((bottom density - surface density)/water depth), was determined for each station for each transect and plotted. Bulk stratification represents a first order approximation of the resistance of the water column to wind and tidal mixing (Pond and Pickard 1983). Bulk stratification was compared for the shelf waters between dates using the non-parametric Kruskal-Wallis test.

All ichthyoplankton were removed from whole plankton samples and identified to lowest possible taxon. Two taxa were used to represent the assemblages found on the

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inner Continental Shelf (ICS) and the Chesapeake Bay mouth (based on criteria in chapter 1, and assemblages derived in chapter 2). The two indicator taxa were *Anchoa* spp (bay-spawned), and *Etropus microstomus* (shelf-spawned, shelf-dependent). The cross-shelf distributions of Atlantic croaker, *Micropogonias undulatus*, shelf-spawned estuarine-dependent, (Norcross 1983), and *Symphurus* spp bay-spawned, (Olney 1976), a member of shelf assemblage (Olney 1996) were compared with the distributions of the two indicator taxa to see if cross-frontal patterns reflected just two potential sources (bay or shelf). Larvae of the four taxa were measured to the nearest 0 1 mm total length (TL) for pre-flexion larvae and standard length (SL) for flexion and post-flexion larvae using the OPTIMAS image analysis system (BioScan, Inc Edmonds, WA) No correction for shrinkage was applied.

Relative larval abundance for each taxa was plotted after standardizing by distance from the front. For this standardization the plume-shelf front was used as the 0 km starting point, stations seaward of the front were positive distances, while bayward stations were plotted as negative distance. Cross-shelf larval densities were examined for serial auto-correlations (NCSS, Kaysville UT) and then subjected to a Spearman rank correlation to test the association between larval abundance and hydrographic variables. To account for the multiple correlations, a Bonferroni adjustment was applied to determine appropriate significance (0 05/8 correlations). For this study, α=0 006 for the correlation analysis. To determine whether larvae were surface-dwelling, the density of larvae was compared between 1m and 3m for each of the four taxa and for total ichthyoplankton using Wilcoxons Sign test. This test was performed independently for each sampling date.

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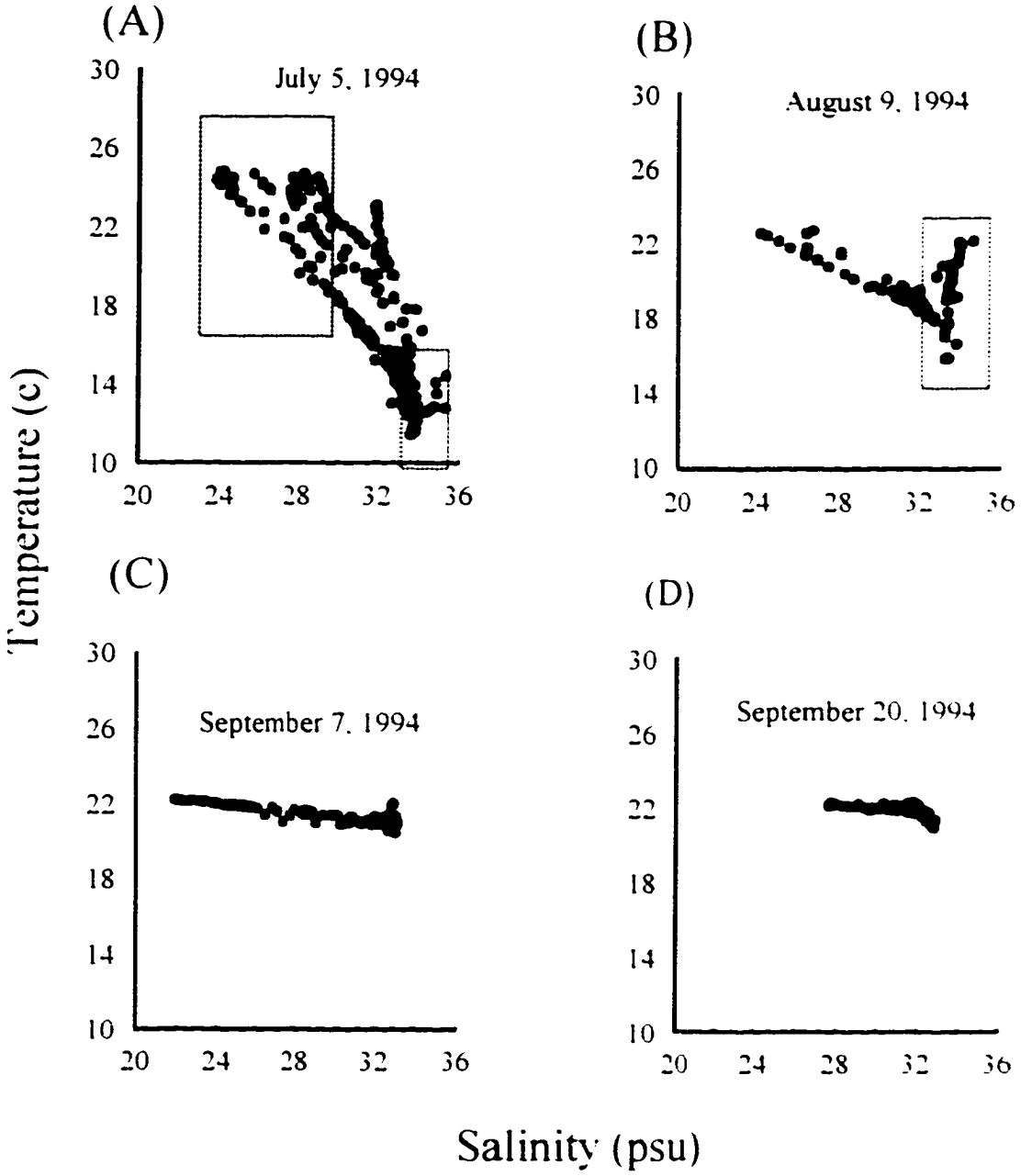

Figure 11 Temperature -vs - salinity (T-S) profiles for each sampling date (A) July 5, large box surrounds plume water with salinities <30 and the small box surrounds Mid-Atlantic shelf water with salinities >32, (B) August 9, box surrounds mid-Atlantic shelf waters with salinities >32, (C) September 7, (D) September 20

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Cross-shelf distributions of ontogenetic stages for each taxa were examined by plotting the proportion of larvae in each length class by station, and used to obtain a qualitative understanding of dispersal and retention across the front

Results

Hydrographic Conditions

Temperature and salinity (T-S) relationships observed during the summer of 1994 reflect oceanographic conditions that were related principally to changing meteorological forcing with advancing season. Especially evident were hydrographic differences related to upwelling and downwelling favorable conditions. For example, three identifiable water masses were present over the shelf on July 5 (Fig. 11a): plume water (<30 psu and <18 °C), inner shelf (near-coastal) waters with salinities in excess of 30 psu and a wide range of temperatures, and mid-Atlantic shelf water with salinities in excess of 32 psu and temperatures ranging from 12 to 18 °C. On August 9, two water masses were visible on the shelf: mixed water from the plume and inner shelf (<32 psu) and mid-Atlantic shelf water (>32 psu) of relatively uniform temperature (Fig. 11b).

T-S relationships showed that temperature was nearly constant across the shelf (<18 °C) on the remaining two cruises (Sept. 7 and Sept. 20). This indicates that density differences on the shelf were defined by salinity (Fig. 11c, 11d).

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Table 7. Summary statistics of bulk stratification across the shelf by sampling date. Kruskal-Wallis Statistic = 17.88, d. f. = 8, T- statistic (T> chi-square) < 0.0001.

Date	Count	Mean	Std. Deviation
5-July-94	10	0.445	0.227
9-Aug.-94	9	0.09	0.101
7-Sept.-94	11	0.096	0.137
20-Sept.-94	10	0.066	0.047

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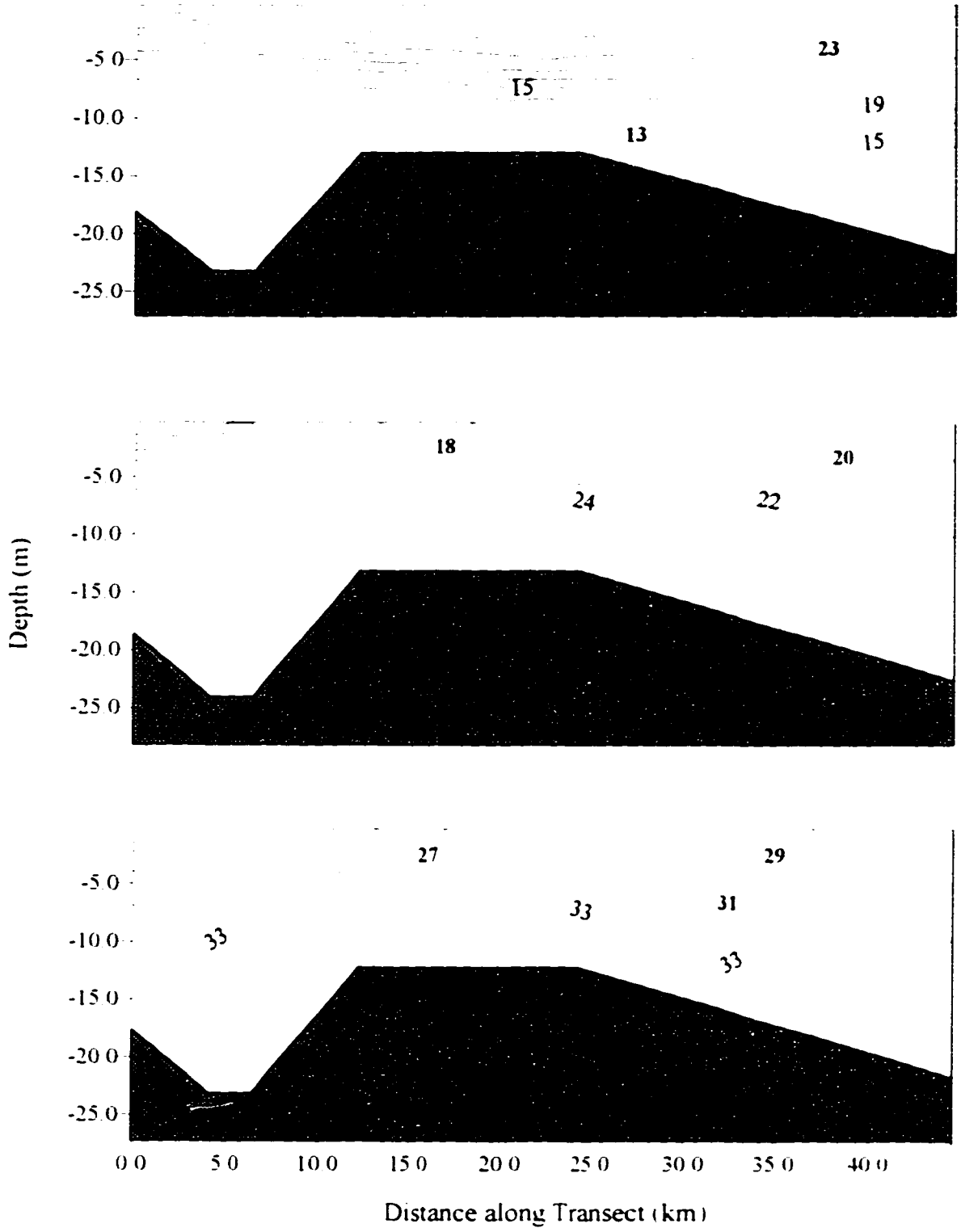

Figure 12. Contour plots of hydrographic variables across the shelf on July 5, 1994 (A) Temperature (^{0}C), (B) Density (σ-t), (C) salinity (psu)

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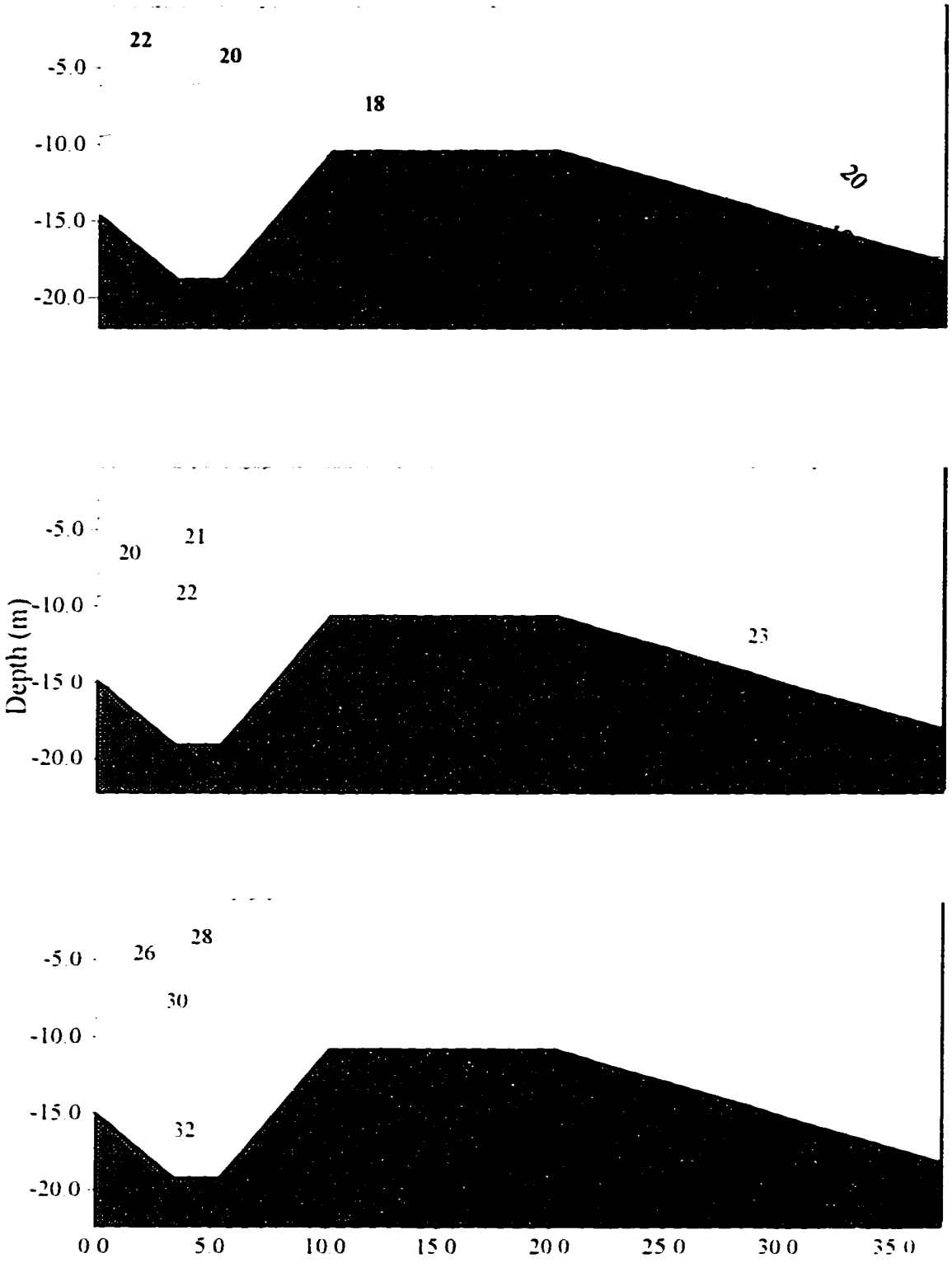

Figure 13 Contour plots of hydrographic variables across the shelf on August 9, 1994 (A) Temperature (^{0}C), (B) Density (σ-t), and (C) salinity (psu)

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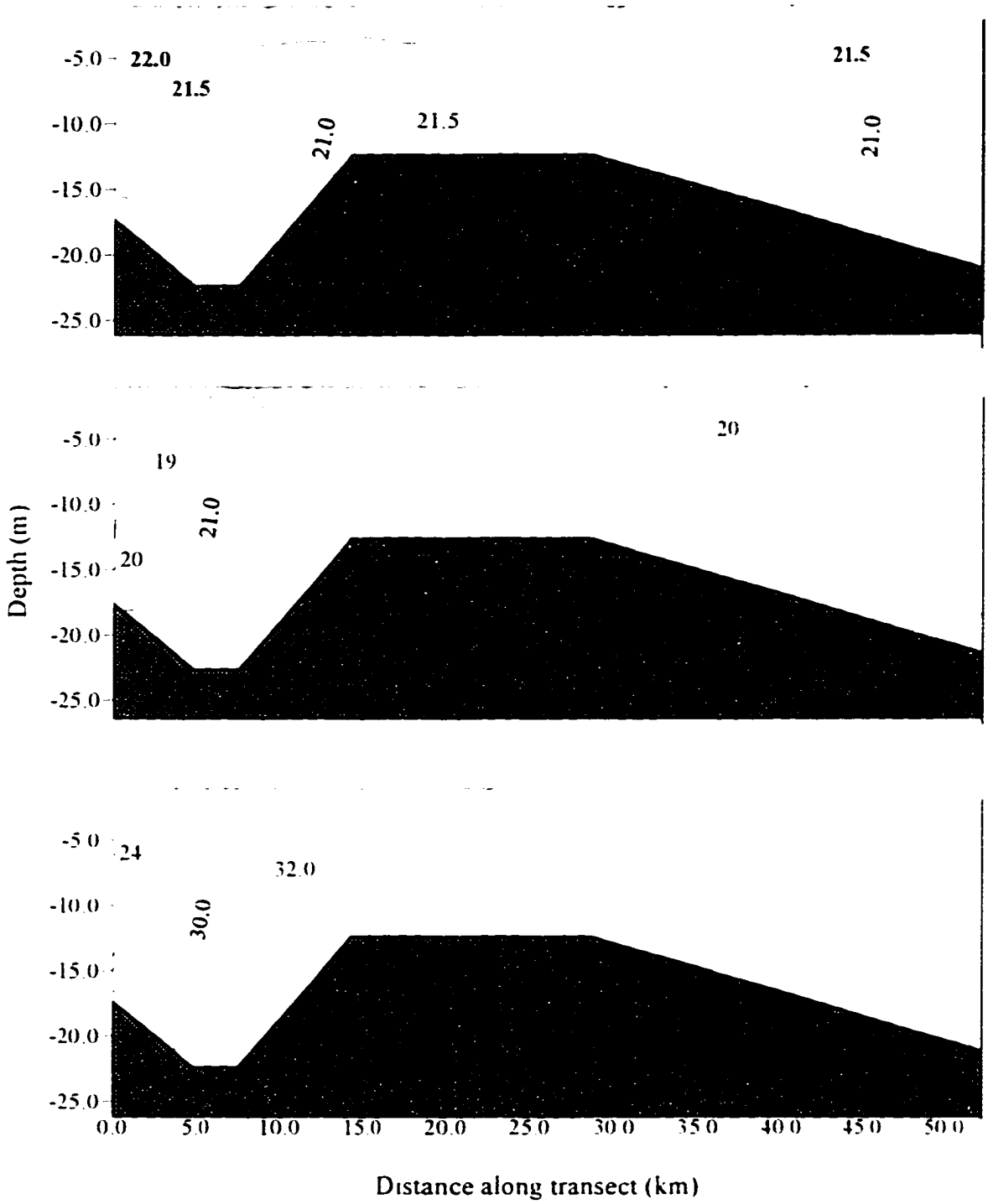

Figure 14 Contour plots of hydrographic variables across the shelf on September 7, 1994 (A) Temperature (^{0}C), (B) Density (σ-t), and (C) Salinity (psu)

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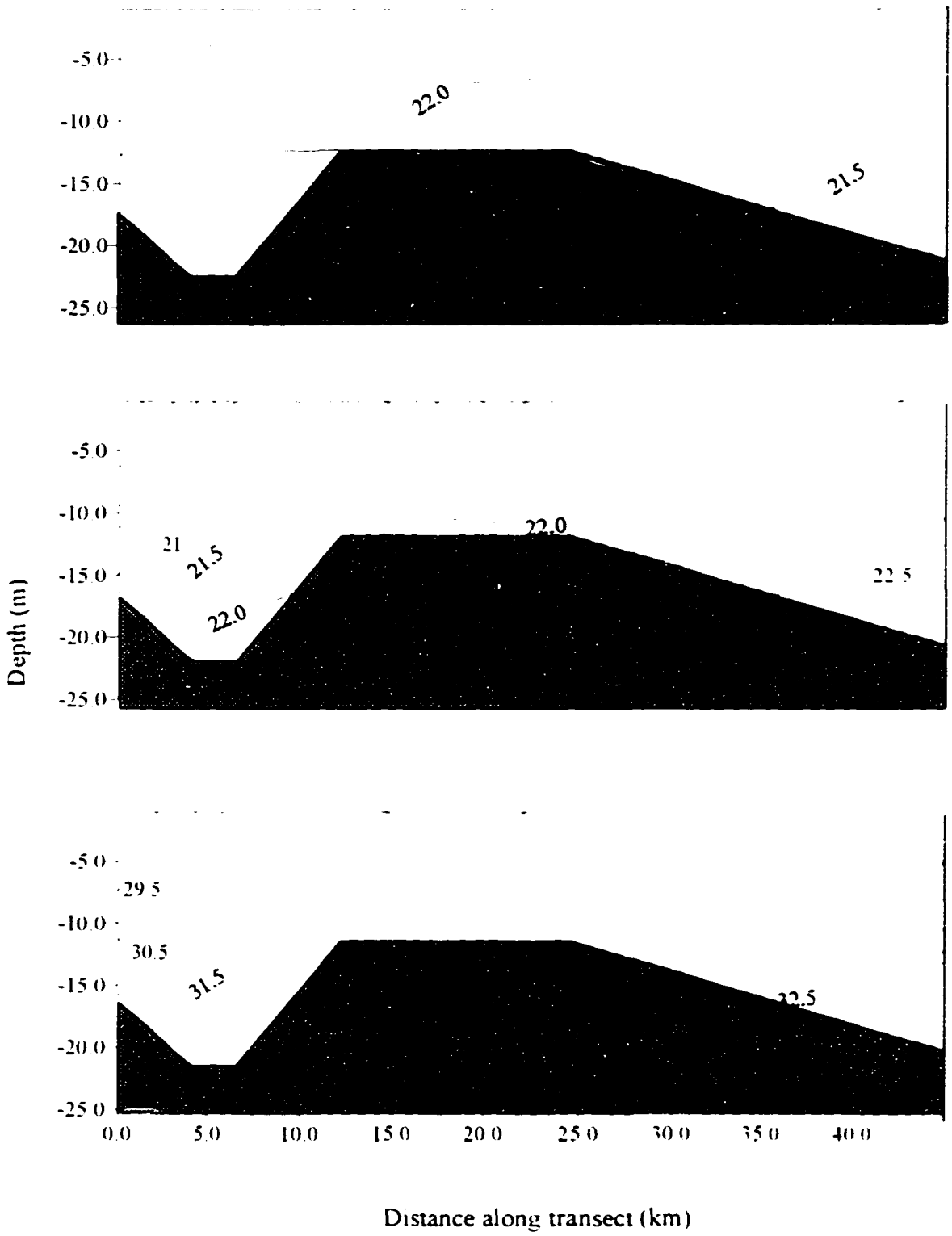

Figure 15. Contour plots of hydrographic variables across the shelf on September 20, 1994. (A) Temperature (^{o}C), (B) Density (σ-t), and (C) Salinity (psu)

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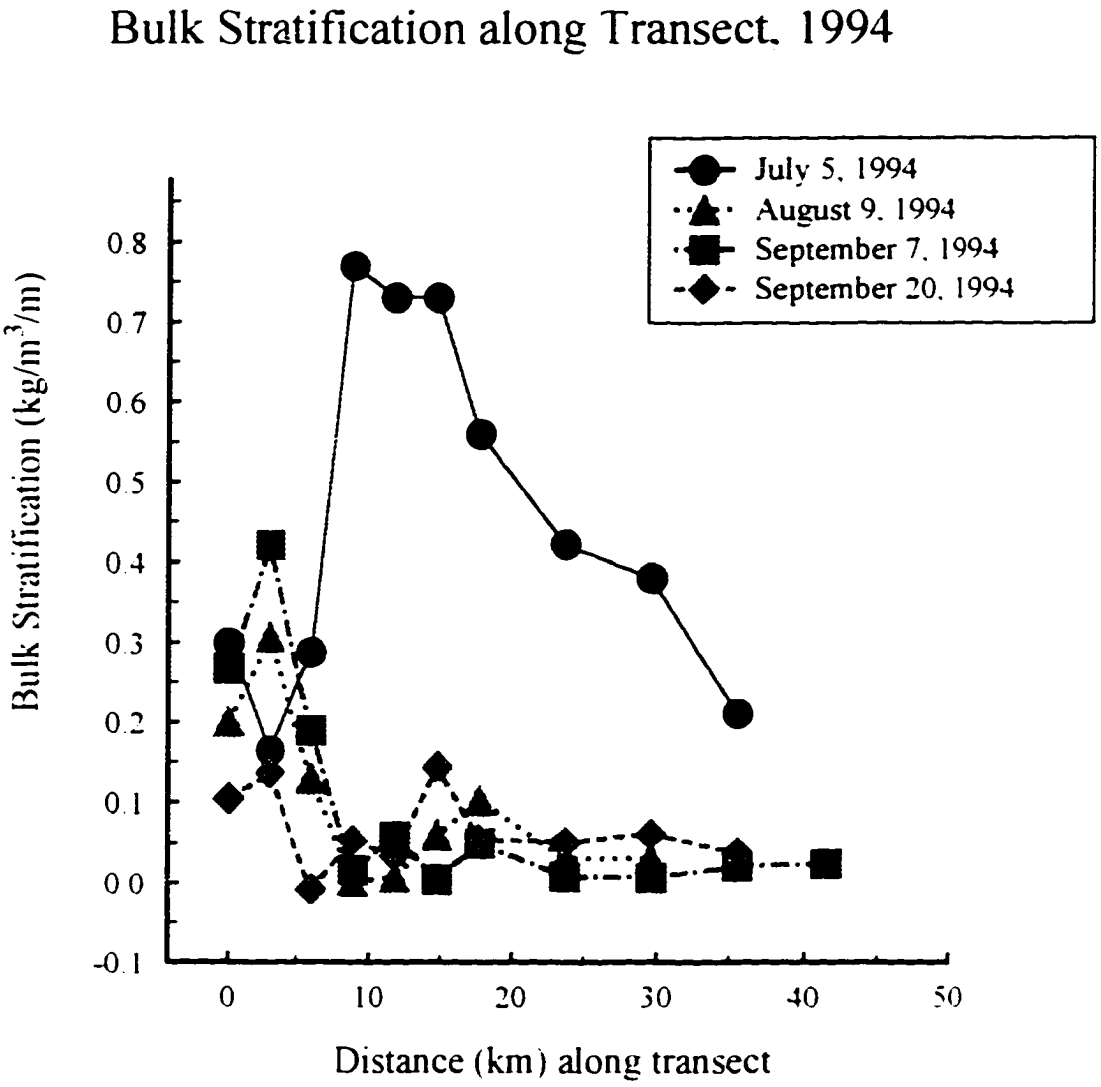

Figure 16 Bulk stratification along the sampling transect on each date High values indicate low potential for mixing Low values indicate that water column is relatively well mixed

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Water Column Structure

The water column was highly stratified on July 5, with a strong, shallow pycnocline inshore (<4m) that increased to >7m at the offshore locations (Fig 12a-c) Two salinity fronts were visible in surface waters (Fig. 12b), an inshore front at 15 km that delineated water less than 29 psu. This inshore front was demarcated by flotsam and a strong foam line. The second salinity front occurred at 41 5 km, and was not demarcated by either flotsam or foam, but was indicated by a slick surface appearance on the ocean This seaward front separated water >29 psu from water >30 psu Temperature maxima were measured in the waters between the two fronts (Fig 12c)

On August 9, most of the temperature and salinity gradients occurred inshore of 15 km. The plume was deep (10m) and compressed against the coast (Fig 13a-c) The salinity front (30 psu) was well defined and occurred approximately 5 2 km along the transect. Waters seaward of the front were well mixed and showed little vertical salinity structure (Fig. 13a) Salinity increased gradually in both surface and bottom waters seaward of the front.

Temperature along the transect on Aug 9 showed considerable vertical structure within the plume (Fig. 13b) Warm plume water was separated from cooler shelf water by the plume front Seaward of the front, the vertical temperature structure comprised an area of nearly isothermal water with properties like mid-Atlantic shelf water (< 33) The pycnocline was compressed against the coast and intersected the surface at the front (Fig 13c) Strong isopleths of density occurred across the plume to the front (5 2 km) Seaward of the plume front there was little density structure and densities were <23 σ-t High density shelf water was evident at the more seaward stations

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Salinity and density structure on the shelf was similar during both September cruises (Fig 14 a, c; Fig. 15 a, c). The plume was confined to the coast inshore of 7.5 km (Fig. 14a-c, 15a-c). On September 7, the 30 psu isopleth surfaced at the front (Fig 14a), but low salinity water was present on the shelf seaward of the front. Higher salinity water was evident at depth at several locations along these transects, but there was no evidence of any cohesive high salinity intrusions, like the event that was sampled on July 5. Most of the density structure was also confined to the plume during these cruises (Fig 14b, 15b). Mixed water with densities >21 σ-t units encompassed the shallow water seaward of the front. Temperature structure across the transects in September was similar to the pattern observed for salinity (Fig. 14b, 15b). Most of the vertical structure was associated with the plume. Seaward of the front water column temperatures were warm nearly isothermal (>21 degrees).

Bulk-Stratification

Bulk stratification varied across the shelf from July through September and was highest within the plume (Fig 16). Mean bulk stratification on each date ranged from 0.06 to 0.445 kg/m^3, with no apparent seasonal trend. On July 5, bulk stratification remained high across the shelf reflecting the highly stratified water column. Over the rest of the summer, bulk stratification was greatest within the plume and decreased seaward of the front. Comparison of bulk stratification by date indicated that the water column on July 5 was significantly more stratified than the other dates (Table 7). These data suggest that, in general, water seaward of the front on the inner-shelf is well mixed unless some meteorological or oceanographic condition forces the plume across the shelf creating local

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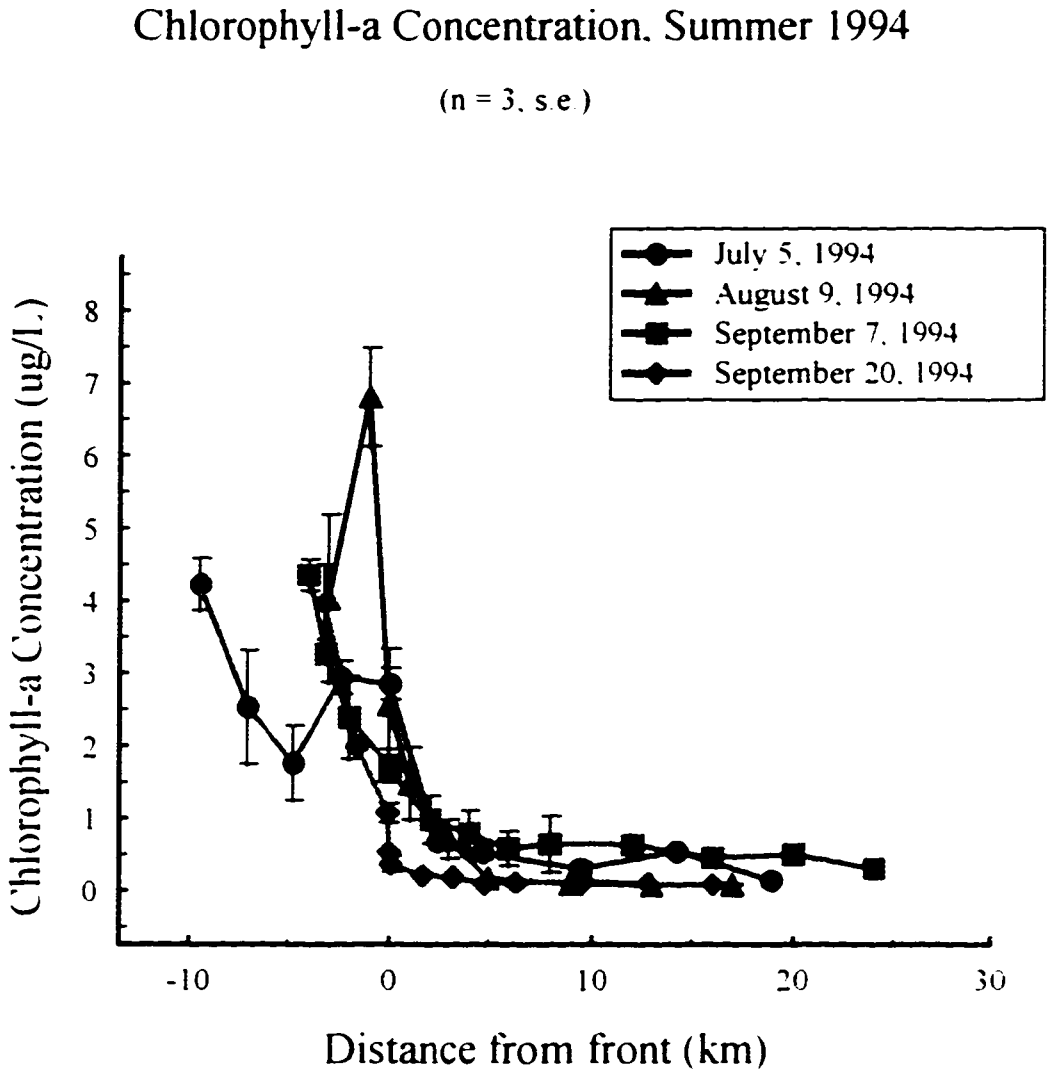

Figure 17 Mean chlorophyll-a concentration (µg/L) across the transect during the four cruise periods Distance is standardized across the front (0 km) Peaks are visible just inshore of the frontal zone on the July 5 and August 9 transects

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Table 8. Ranked mean density (#/100m^3) of ichthyoplankton collected during summer, 1994 (n=73).

Variable	Mean	Std. Deviation	Maximum
Micropogonias undulatus	22.73	82.00	627.00
Anchoa spp.	18.25	95.10	791.00
Prionotus spp.	5.05	10.90	65.30
Etropus microstomus	3.27	6.88	30.10
Ophidion spp.	1.56	4.28	20.56
Menticirrhus spp.	1.35	2.74	10.87
Symphurus spp.	1.20	3.43	19.70
Blenniidae	0.82	1.66	10.56
Cynoscion regalis	0.48	2.94	23.10
Anchoa post-larvae	0.33	1.73	13.62
Gadidae	0.24	0.69	4.50
Gobiidae	0.22	1.27	10.79
Peprilus triacanthus	0.22	0.62	3.25
Gobiesox strumosus	0.18	0.74	5.35
Unknown (Hare #50)	0.16	0.55	3.85
Astroscopus guttatus	0.16	0.58	4.70
Atherinidae	0.12	0.68	5.48
Centropristis striata	0.12	0.66	5.49
Syngnathus fuscus	0.09	0.28	1.92
Trinectes maculatus	0.07	0.45	3.78
Tetraodontidae	0.06	0.23	1.69
Scombridae	0.05	0.17	1.05
Bothus spp.	0.04	0.17	1.06
Cynoscion nebulosus	0.03	0.17	1.13
Synodus foetens	0.03	0.22	1.92
Hippocampus spp.	0.03	0.10	0.58
Citharichthys arctifrons	0.01	0.04	0.29
Myrichthys novacula	0.01	0.04	0.26
Hemiramphidae	0.01	0.04	0.28
Glyptocephalus spp.	<0.01	0.03	0.26
Anguilla leptocephalus	<0.01	0.03	0.25
Monacanthidae	<0.01	0.02	0.17
Carangidae	<0.01	0.01	0.08

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stratification where there usually is none.

Chlorophyll-a

Maximal concentrations of chlorophyll-a (chl-a) always occurred within the plume although the magnitude of the peaks varied between dates. There were no enhanced chl-a concentrations associated with the front (Fig. 17). On July 5 and August 9, chlorophyll-a concentrations were increased at stations just inshore of the plume front. Differences in chl-a concentrations between the stations just inside and just outside the front varied between sampling dates. On July 5, the difference in chl-a across the front was 1.5 µg/l, while on August 9 the difference was 4.5 µg/l. Chlorophyll-a concentrations were always low (<1.0 µg/l) seaward of the plume front, and there was never any peaks in chl-a offshore. These data indicate that chl-a was retained within the plume defined by the 30 psu isopleth.

Seasonal Patterns of Ichthyoplankton

Thirty-three taxa were caught during the summer of 1994 (Table 8), and the two indicator taxa used in this study (*Anchoa* spp. and *E. microstomus*) ranked among the seven most abundant larvae collected. Seasonal patterns were exhibited by *Anchoa* spp. and *M. undulatus*. *Anchoa* spp. was most abundant early in the season (July and August) while *M. undulatus* increased in abundance through the summer. Overall these two taxa ranked highest in mean summer abundance (Table 8).

Significant seasonal correlations were found between the two indicator taxa (*Anchoa* spp. and *E. microstomus*), *M. undulatus*, *Symphurus* spp. and environmental parameters at 1m. *Anchoa* spp. was negatively correlated with salinity and distance from the front, but positively correlated with both chlorophyll-a and bulk stratification. This

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reflects the association of *Anchoa* spp with the plume (Table 9) *Etropus microstomus*, the indicator of the shelf assemblage was negatively correlated with chlorophyll-a ($r=-0.4630$, $p<0.0015$), and positively correlated with salinity ($r=0.4701$, $p<0.0013$) reflecting its shelf association. *Micropogonias undulatus*, the shelf-spawned, estuarine-dependent taxon was positively correlated with *E. microstomus* ($r=0.4688$, $p<0.0013$), but was not significantly correlated with any other parameter. *Symphurus* spp was not correlated with any taxa or environmental parameter for the summer on the whole at the surface, even though it is known to spawn within the plume and the baymouth

At 3m seasonal correlations were similar to the correlations observed at 1m (Table 10). *Anchoa* spp was positively correlated with chlorophyll-a ($r=0.5921$, $p<0.0008$) *Micropogonias undulatus* was correlated with *E. microstomus* ($r=0.5355$, $p<0.0030$) In addition to being correlated with *M. undulatus*, *E. microstomus* was positively correlated with distance from the front ($r=0.6289$, $p<0.0004$) and negatively correlated with chlorophyll-a ($r=-0.5444$, $p<0.0025$) showing a clear association with shelf waters *Symphurus* spp. was not correlated with any parameter at 3m

Cross-frontal ichthyoplankton distributions

July 5 Seventeen taxa were collected during this cruise, but only three taxa were abundant (>1.0/100m^3) (Table 11) Within the plume, exceptional densities of *Anchoa* spp were recorded (>1300/100m^3), while seaward of the inshore front very few larvae were caught. *Etropus microstomus* were uncommon (<0.5/100m^3) and only occurred at the most seaward stations (Fig. 18)

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Table 9. Spearmans correlations between taxa and environmental parameters at 1m, summer 1994 (n=44). Bonferroni adjustment for multiple comparisons is used to adjust α. The resulting significance level is 0.006. The upper number in the matrix is the r-value and the lower number is the significance (p). Significant correlation's and their respective probabilities are highlighted in bold.

	Anchoa spp.	*Symphurus* spp	*Micropogonias undulatus*	*Etropus microstomus*
Anchoa spp	1	0.10741	-0.36338	-0.21306
	0	0.4877	0.0153	0.165
Symphurus spp	0.10741	1	0.1791	0.15858
	0.4877	0	0.2447	0.3039
Micropogonias undulatus	-0.36338	0.1791	1	0.46886
	0.0153	0.2447	0	0.0013
Etropus microstomus	-0.21306	0.15858	**0.46886**	1
	0.165	0.3039	**0.0013**	0
Salinity 1m	**-0.52519**	-0.18281	0.15472	**0.47019**
	0.0003	0.2349	0.316	**0.0013**
Chlorophyll-a	**0.6262**	0.22879	-0.18734	**-0.46306**
	<0.0001	0.1352	0.2233	**0.0015**
Frontal Distance	**-0.50451**	-0.32139	0.13152	0.39621
	0.0005	0.0334	0.3948	0.0078
Bulk Stratification	**0.6179**	0.12707	**-0.42103**	-0.32391
	<0.0001	0.4111	**0.0044**	0.032

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Table 10 Spearmans correlations between taxa and environmental parameters at 3m, summer 1994 (n=29). Bonferroni adjustment for multiple comparisons is used to adjust α. The resulting significance level is 0.006. The upper number in the matrix is the r-value and the lower number is the significance (p). Significant correlation's and their respective probabilities are highlighted in bold.

	Anchoa spp.	*Symphurus* spp.	*Micropogonias undulatus*	*Etropus microstomus*
***Anchoa* spp.**	1	-0.13795	-0.33933	-0.33925
	0	0.4755	0.0717	0.0718
***Symphurus* spp**	-0.13795	1	0.22745	-0.18609
	0.4755	0	0.2354	0.3338
Micropogonias undulatus	-0.33933	0.22745	1	0.53556
	0.0717	0.2354	0	0.0028
Etropus microstomus	-0.33925	-0.18609	**0.53556**	1
	0.0718	0.3338	**0.0028**	0
Salinity 3m	-0.22814	-0.41508	-0.06963	0.30308
	0.2339	0.0252	0.7197	0.11
Chlorophyll-a	**0.59218**	0.32272	-0.02198	**-0.54448**
	0.0007	0.0877	0.9099	**0.0023**
Frontal Distance	-0.30932	-0.4752	0.18272	**0.62898**
	0.1025	0.0092	0.3428	**0.0003**
Bulk Stratification	0.11938	0.1618	-0.29877	-0.25001
	0.5374	0.4017	0.1154	0.1909

Table 11. Ranked mean density of larvae collected during the summer of 1994 on each of four sampling dates, July 5, August 9, September 7, September 20.

	July 5			August 9		
Variable	**Mean**	**Std. Deviation**	**Maximum**	**Mean**	**Std. Deviation**	**Maximum**
Anchoa post-larvae	0.00	0.00	0.00	0.00	0.00	0.00
Anchoa spp.	173.03	341.75	1318.00	11.64	20.80	81.08
Anguilla leptocephalus	0.00	0.00	0.00	0.00	0.00	0.00
Astroscopus guttatus	0.03	0.09	0.30	0.09	0.20	0.77
Atherinidae	0.02	0.08	0.34	0.00	0.00	0.00
Blenniidae	1.78	2.68	9.70	1.08	2.94	10.56
Bothus spp.	0.00	0.00	0.00	0.02	0.09	0.41
Carangidae	0.01	0.03	0.15	0.00	0.00	0.00
Centropristis striata	0.00	0.00	0.00	0.03	0.08	0.27
Citharichthys arctifrons	0.01	0.03	0.15	0.02	0.08	0.29
Cynoscion regalis	6.34	15.64	58.82	0.12	0.32	1.13
Cynoscion nebulosus	0.00	0.00	0.00	1.46	2.27	7.52
Etropus microstomus	0.01	0.06	0.27	1.33	2.62	10.82
Gadidae	0.00	0.00	0.00	0.00	0.00	0.00
Glyptocephalus spp.	0.00	0.00	0.00	0.00	0.00	0.00
Gobiosox strumosus	0.99	2.80	12.25	0.62	1.37	5.35
Gobiidae	0.00	0.00	0.00	0.07	0.18	0.77
Hemiramphidae	0.00	0.00	0.00	0.01	0.06	0.28
Hippocampus spp.	0.09	0.23	0.74	0.06	0.17	0.58
Menticirrhus spp.	0.13	0.48	2.10	1.34	2.57	9.61
Micropogonias undulatus	0.00	0.00	0.00	0.75	2.19	9.61
Monacanthidae	0.02	0.08	0.34	0.00	0.00	0.00
Ophidion spp.	0.00	0.00	0.00	0.35	0.63	2.16
Peprilus triacanthus	0.39	1.02	3.30	0.45	0.83	3.18
Prionotus spp.	0.00	0.00	0.00	2.62	3.84	13.46
Scombridae	0.05	0.18	0.82	0.17	0.33	1.05
Symphurus spp.	0.20	0.60	2.45	1.35	1.99	6.48
Syngnathus fuscus	0.02	0.08	0.34	0.39	1.20	5.00
Synodus spp.	0.00	0.00	0.00	0.10	0.44	1.92
Tetraodontidae	0.03	0.08	0.34	0.04	0.19	0.85
Trinectes maculatus	0.00	0.00	0.00	0.25	0.87	3.78
Unknown (Hare # 50)	0.00	0.00	0.00	0.39	0.93	3.85
Xyrichtys novacula	0.00	0.00	0.00	0.01	0.06	0.25

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Table 11 - continued.

	September 7			September 20		
Variable	**Mean**	**Std. Deviation**	**Maximum**	**Mean**	**Std. Deviation**	**Maximum**
Anchoa post-larvae	1.24	3.20	13.62	0.00	0.00	0.00
Anchoa spp.	0.18	0.62	2.63	0.51	0.70	2.45
Anguilla leptocephalus	0.01	0.06	0.25	0.00	0.00	0.00
Astroscopus guttatus	0.18	0.33	1.02	0.25	0.92	4.70
Atherinidae	0.01	0.07	0.32	0.56	1.52	6.23
Blenniidae	0.74	0.90	3.38	0.74	0.89	3.90
Bothus spp.	0.04	0.18	0.82	0.06	0.22	1.06
Carangidae	0.00	0.00	0.00	0.16	0.57	2.41
Centropristis striata	0.34	1.22	5.49	0.08	0.24	1.20
Citharichthys arctifrons	0.00	0.00	0.00	0.00	0.00	0.00
Cynoscion regalis	0.00	0.00	0.00	0.00	0.00	0.00
Cynoscion regalis	0.00	0.00	0.00	0.00	0.00	0.00
Etropus microstomus	7.09	9.48	25.97	2.76	6.71	30.10
Gadidae	0.56	0.77	2.45	0.25	0.89	4.50
Glyptocephalus spp.	0.00	0.00	0.00	0.01	0.05	0.26
Gobiosox strumosus	0.00	0.00	0.00	0.09	0.21	0.86
Gobiidae	0.04	0.17	0.80	0.56	2.11	10.79
Hemiramphidae	0.00	0.00	0.00	0.01	0.04	0.21
Hippocampus spp.	0.00	0.00	0.00	0.01	0.06	0.32
Menticirrhus spp.	0.48	1.08	4.38	2.39	3.71	10.87
Micropogonias undulatus	26.33	56.80	218.20	43.03	126.24	627.00
Monacanthidae	0.00	0.00	0.00	0.00	0.00	0.00
Ophidion spp.	4.59	7.17	20.56	0.50	1.74	8.18
Peprilus triacanthus	0.01	0.05	0.24	0.17	0.40	1.60
Prionotus spp.	7.95	11.75	38.96	6.14	14.37	65.30
Scombridae	0.00	0.00	0.00	0.00	0.00	0.00
Symphurus spp.	2.80	6.06	19.70	0.43	0.98	4.56
Syngnathus fuscus	0.10	0.26	1.02	0.10	0.21	0.98
Synodus spp	0.00	0.00	0.00	0.01	0.05	0.26
Tetraodontidae	0.15	0.39	1.69	0.00	0.00	0.00
Trinectes maculatus	0.00	0.00	0.00	0.01	0.06	0.30
Unknown (Hare # 50)	0.00	0.00	0.00	0.18	0.42	1.70
Xyrichtys novacula	0.00	0.00	0.00	0.01	0.05	0.26

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Low overall ichthyoplankton abundance (<1 0/100m^3) occurred between the inshore front and the plume-shelf front 15 km seaward *Anchoa* spp showed a significant correlation with distance from the 30 psu front (r=-0 8060, p<0 0050), but not with chl-a or salinity at 1m. Larvae of the remaining taxa were too rare to analyze

August 9: *Anchoa* spp., and *Symphurus* spp were among the five most abundant taxa collected on this date, while *E. microstomus* and *M. undulatus* ranked sixth and eighth, respectively (Table 11) Larvae of the two indicator taxa (*Anchoa* spp and *E. microstomus*) as well as *Symphurus* spp and *M. undulatus* were concentrated within 7 5 km of the front. Peak larval density (total and specific) occurred at stations just seaward and just shoreward of the front at 1m (Fig 19a) A similar pattern of larval peaks was evident at 3m (Fig 19b) Larval densities of total ichthyoplankton, and the four taxa considered in this study were minimal at the front *Anchoa* spp was most abundant within the plume, although some *Anchoa* spp were found seaward of the front (Fig 19b) Densities of *Symphurus* spp exhibited a peak inshore of the front at 3m, while *M. undulatus* and *E. microstomus* were most abundant just offshore of the front Smaller peaks were visible for both taxa approximately 10 km seaward of the front None of the larvae were significantly correlated with each other or the environmental parameters The cross-shelf pattern reflected retention of *Anchoa* spp and *E. microstomus* in plume and shelf waters, respectively The pattern for *Symphurus* spp and *M. undulatus* were less defined

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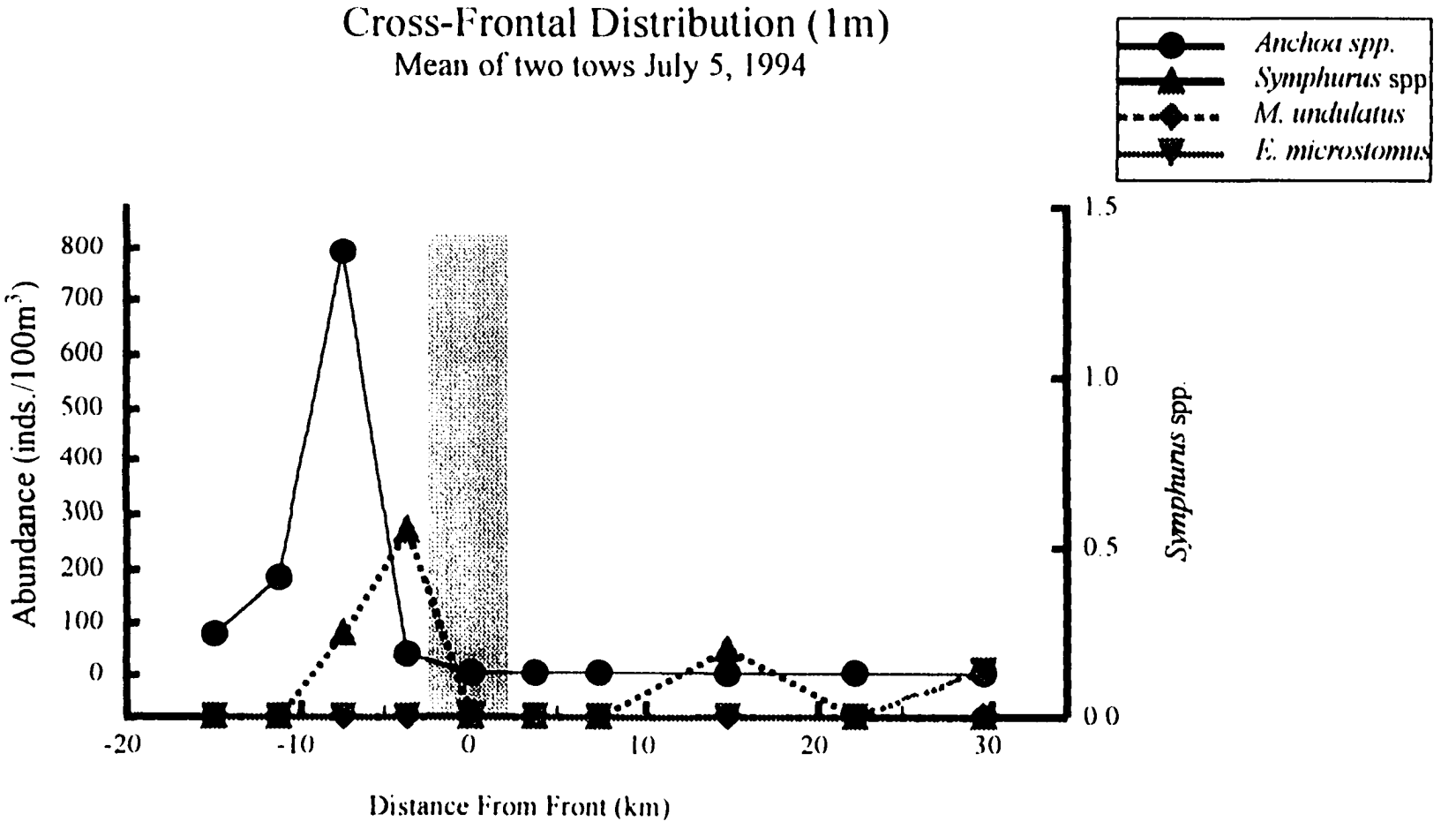

Figure 18 Mean cross-frontal distribution of indicator taxa standardized to distance from the front on July 5 within surface waters *Anchoa* spp is on the primary y-axis and *Symphurus* spp., and *Etropus microstomus* are plotted using the secondary y-axis *Micropogonias undulatus* was not captured during this cruise The frontal station is within the shaded box

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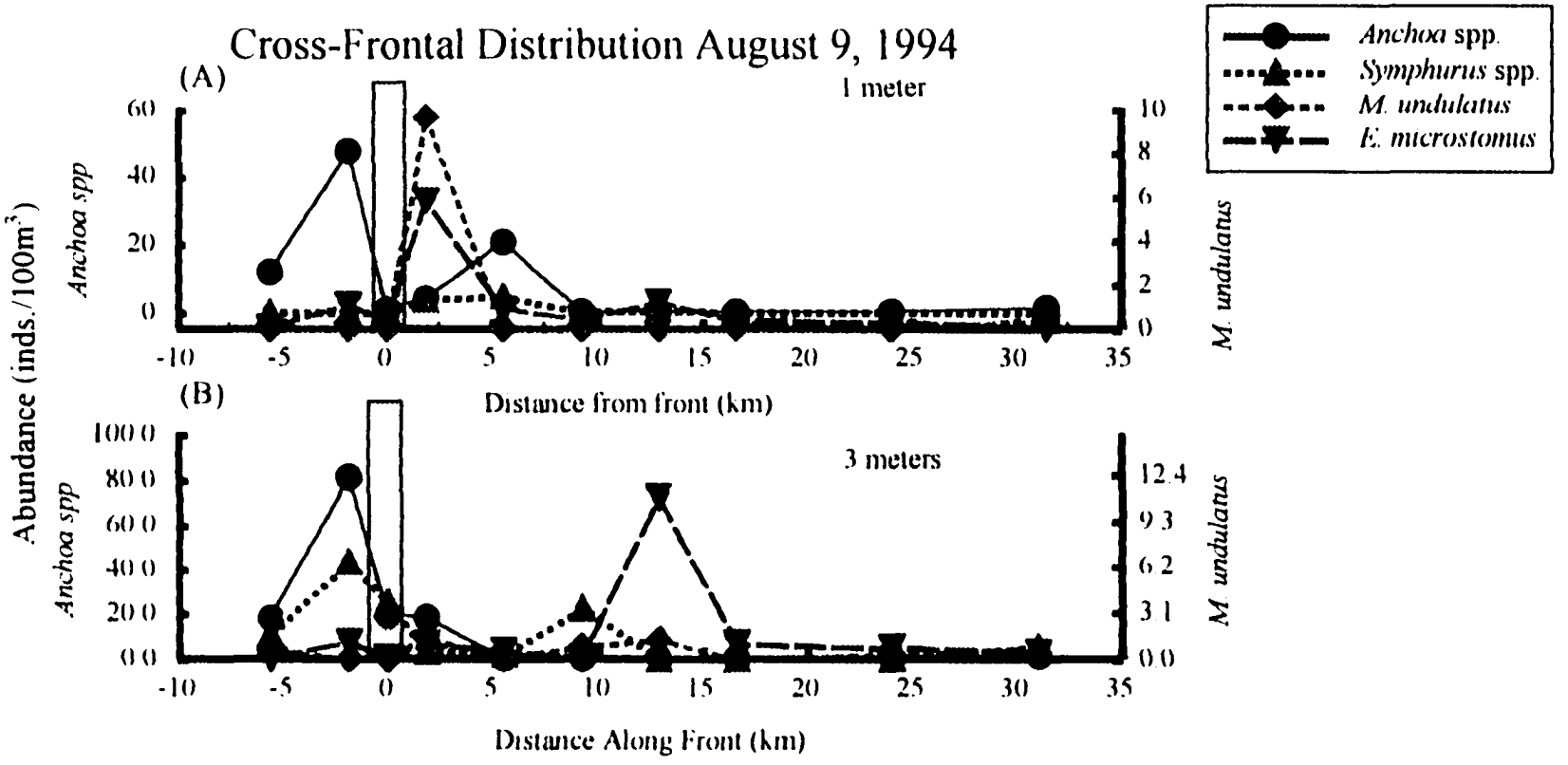

Figure 19 Cross-frontal distribution of indicator taxa standardized to distance from the front during on August 9 at 1m (A) *Anchoa* spp is on the primary y-axis, and the remaining indicator taxa *Symphurus* spp , *Micropogonias undulatus* and *Etropus microstomus* are plotted using the secondary y axis, Cross-frontal distribution of indicator taxa standardized to distance from the front during on August 9 at 3m *Anchoa* spp is on the primary y-axis, and the remaining indicator taxa *Symphurus* spp , *Micropogonias undulatus* and *Etropus microstomus* are plotted using the secondary y-axis (B) The frontal station is within the shaded box

September 7: Twenty-five taxa were collected on this cruise (Table 11) and total larvae,both indicator taxa, as well as *Symphurus* spp., and *M. undulatus* were more abundant at 3m than at the surface ($p < 0.05$, for each taxa) *Micropogonias undulatus* was the most abundant taxa captured on this date, with a maximum abundance >600/100m^3, and a mean abundance of 43/100m^3 *Anchoa* spp and *Symphurus* spp were the eighth and tenth most and exhibited low overall abundance

No larval aggregation was found at the front The four taxa in this study did not show the same strong peaks inshore and offshore of the front (Fig 20a-b) *Anchoa* spp was most abundant in surface tows within the plume, but was also found offshore of the front. In both the surface and 3m tows, there was evidence of a multi-specific larval peak about 10 km seaward of the front This multi-specific peak contained *M. undulatus*, *Anchoa* spp and *E. microstomus* at the surface At 3m, *E. microstomus* and *M. undulatus* dominated the multi-specific peak.

No significant correlations were found between any taxa or environmental parameter in the surface tows At 3m, *E. microstomus* was positively correlated with salinity ($r=0.8560$, $p<0.0040$), distance from the front ($r=0.8188$, $p<0.003$) and negatively correlated with chlorophyll-a ($r=-0.8002$, $p<0.004$) indicating a strong association with shelf waters. The remaining taxa did not exhibit any significant correlations

September 20: On this sampling date total larval density was greater at 3m than at the surface ($p < 0.05$) Of the nineteen taxa collected *Micropogonias undulatus* was the most abundant Both *E. microstomus* and *Symphurus* spp. ranked in the top five while *Anchoa* spp was relatively uncommon (<1.0/100m^3) (Table 11) *Micropogonias undulatus* and *E. microstomus* larvae were more abundant at depth than at the surface ($p < 0.03$, for both

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taxa). Neither *Anchoa* spp. or *Symphurus* spp. showed any significant differences in their depth distributions.

Multi-specific peaks in larval abundance once again occurred at stations just inshore and offshore of the front, while at the front total larval density was again a minima. *Micropogonias undulatus* and *Symphurus* spp. larvae were most abundant at stations just inshore and offshore of the front (Fig. 21a-b). *Anchoa* spp. peaked inshore of the front, but overall abundance was low <2/100m^3. *Etropus microstomus* was most abundant offshore of the front in both surface and 3m samples (Fig. 21 a, b).

Symphurus spp. was negatively correlated with salinity at 1m ($r=-0.7933$, $p=0.0036$). No other significant correlations were found at 1 or 3m. These results suggest that the observed larval distributions were not related to hydrography on this date.

Ontogenetic Patterns

Ontogenetic patterns across the plume front were, in many cases, different than the patterns in larval abundance. For example, nearly all ontogenetic stages of *Anchoa* spp. were retained within the plume throughout the summer. When this taxa was present seaward of the front, the larvae were usually pre-flexion. This pattern suggests that physical translocation of these larvae was responsible for their presence on the shelf.

Differing patterns in the cross-shelf distributions of ontogenetic stages were exhibited by the remaining taxa (*Symphurus* spp., *E. microstomus*, and *M. undulatus*). *Symphurus* spp. showed evidence of ontogenetic an migration across the front on all dates at both depths (Fig. 22a, 22b). On August 9, small larvae (<3.5 mm) occurred within the plume and in the vicinity of the front. Larger larvae (>3.5 mm) were found almost

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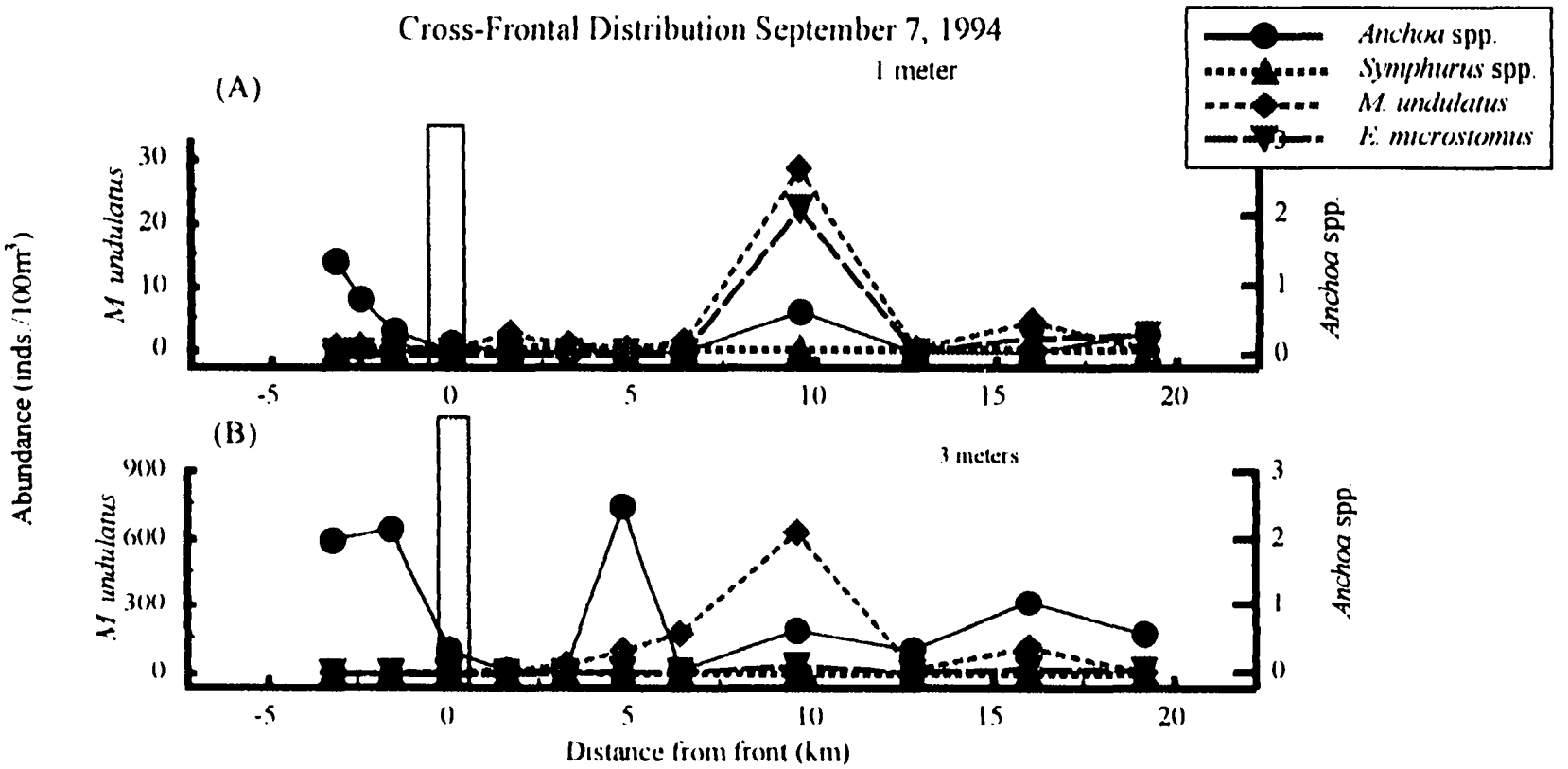

Figure 20 Cross-frontal distribution of indicator taxa standardized to distance from the front during on September 7 at 1m *Anchoa* spp. is plotted using secondary y-axis, and the remaining indicator taxa *Symphurus* spp , *Micropogonias undulatus* and *Etropus microstomus* are plotted using the primary y-axis (A), Cross-frontal distribution of indicator taxa standardized to distance from the front during on September 7 at 3m *Anchoa* spp. is plotted using the secondary y-axis, and the remaining indicator taxa *Symphurus* spp , *Micropogonias undulatus* and *Etropus microstomus* are plotted using the secondary y-axis (B) The frontal station is within the shaded box

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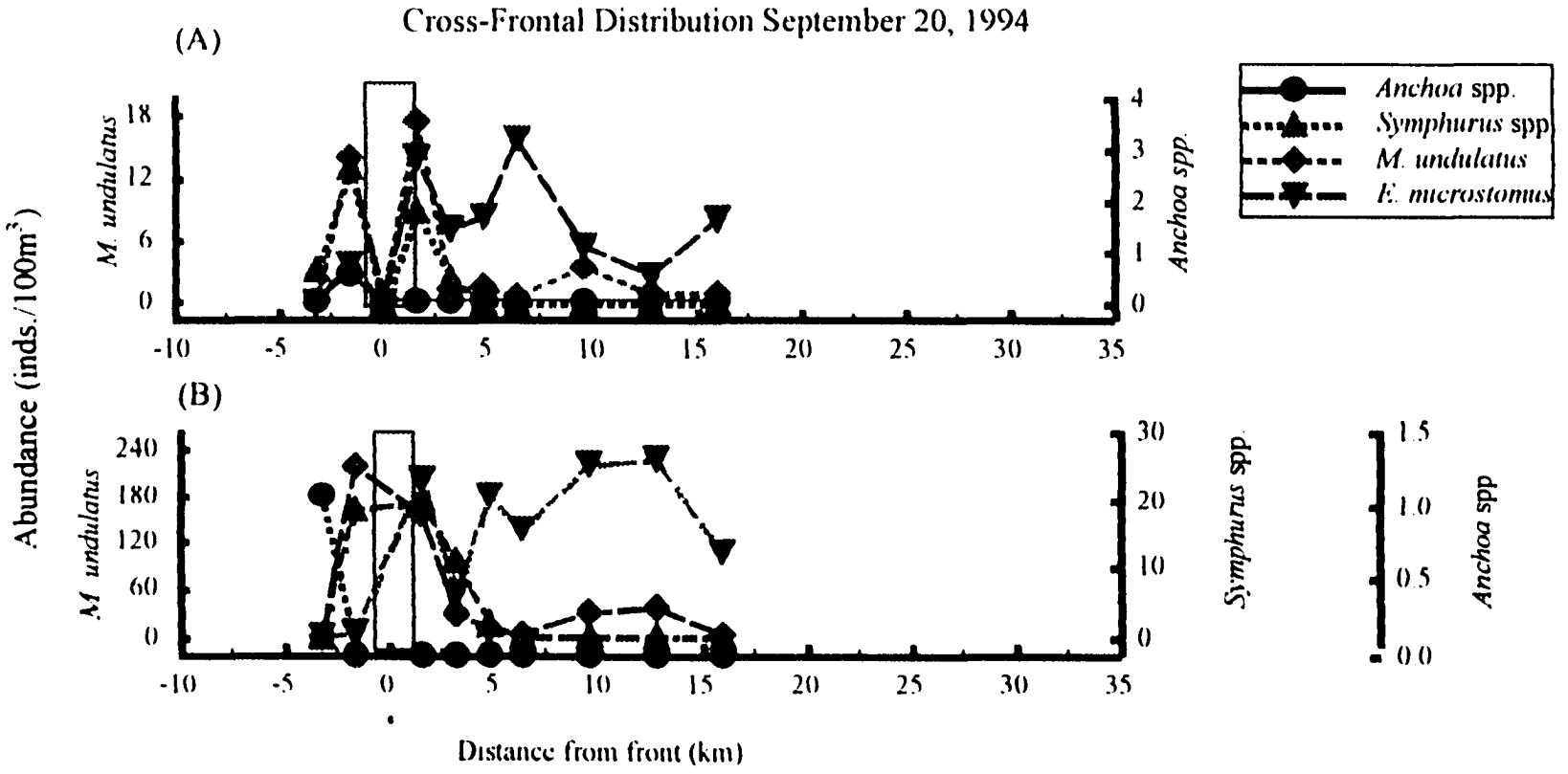

Figure 21 Cross-frontal distribution of indicator taxa standardized to distance from the front during on September 20 at 1m *Anchoa* spp. is plotted using the secondary y-axis, and the remaining indicator taxa *Symphurus* spp., *Micropogonias undulatus* and *Etropus microstomus* are plotted using the primary y-axis (A), Cross-frontal distribution of indicator taxa standardized to distance from the front during on September 20 at 3m *Anchoa* spp. is plotted using the secondary y-axis, and the remaining indicator taxa *Symphurus* spp., *Micropogonias undulatus* and *Etropus microstomus* are plotted using the primary y-axis (B) The frontal station is within the shaded box

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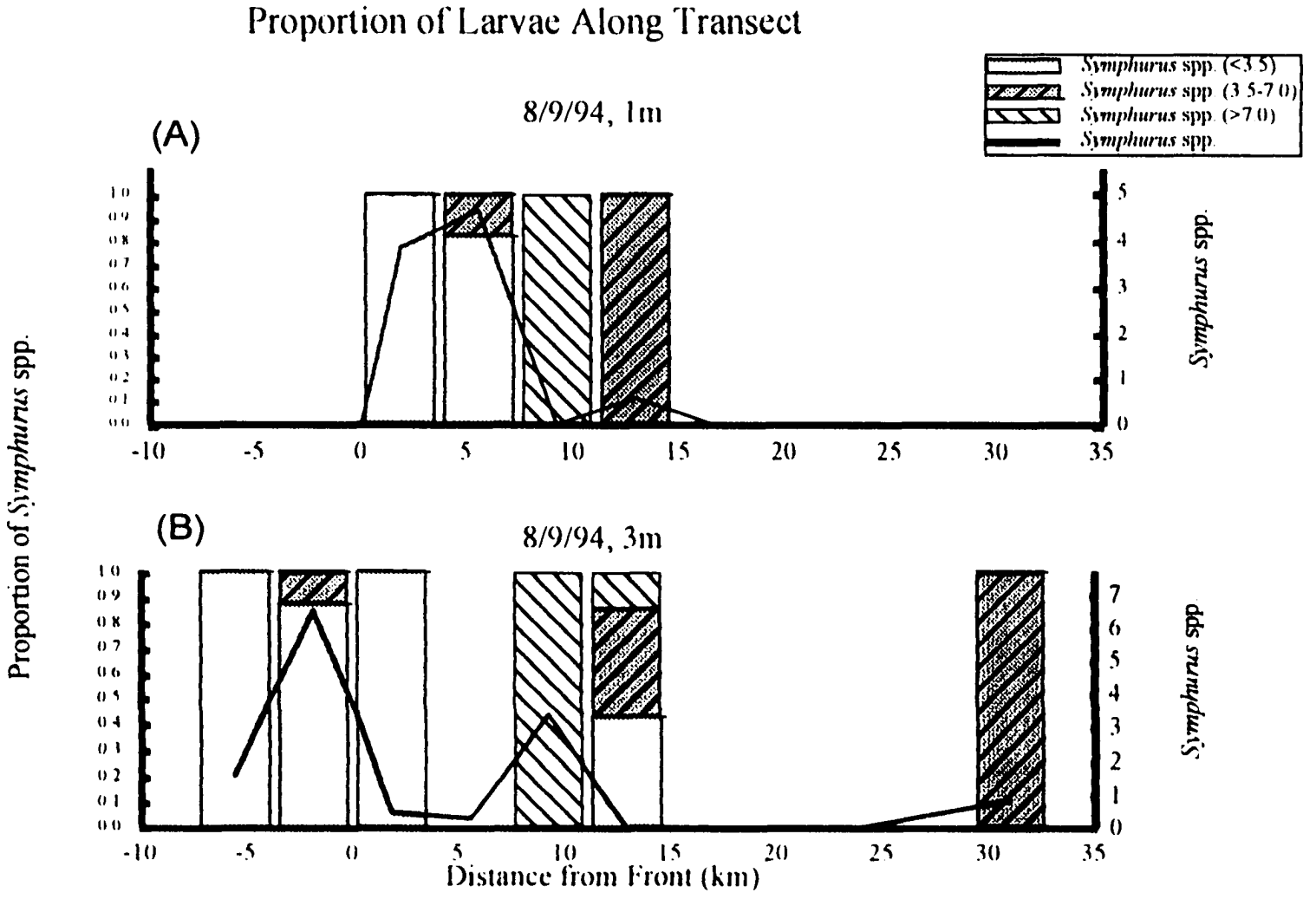

Figure 22 Proportion of ontogenetic stages (bars) and density (#/100m^3) of *Symphurus* spp along the transect on August 9, 1994 (a) 1m, (b) 3m

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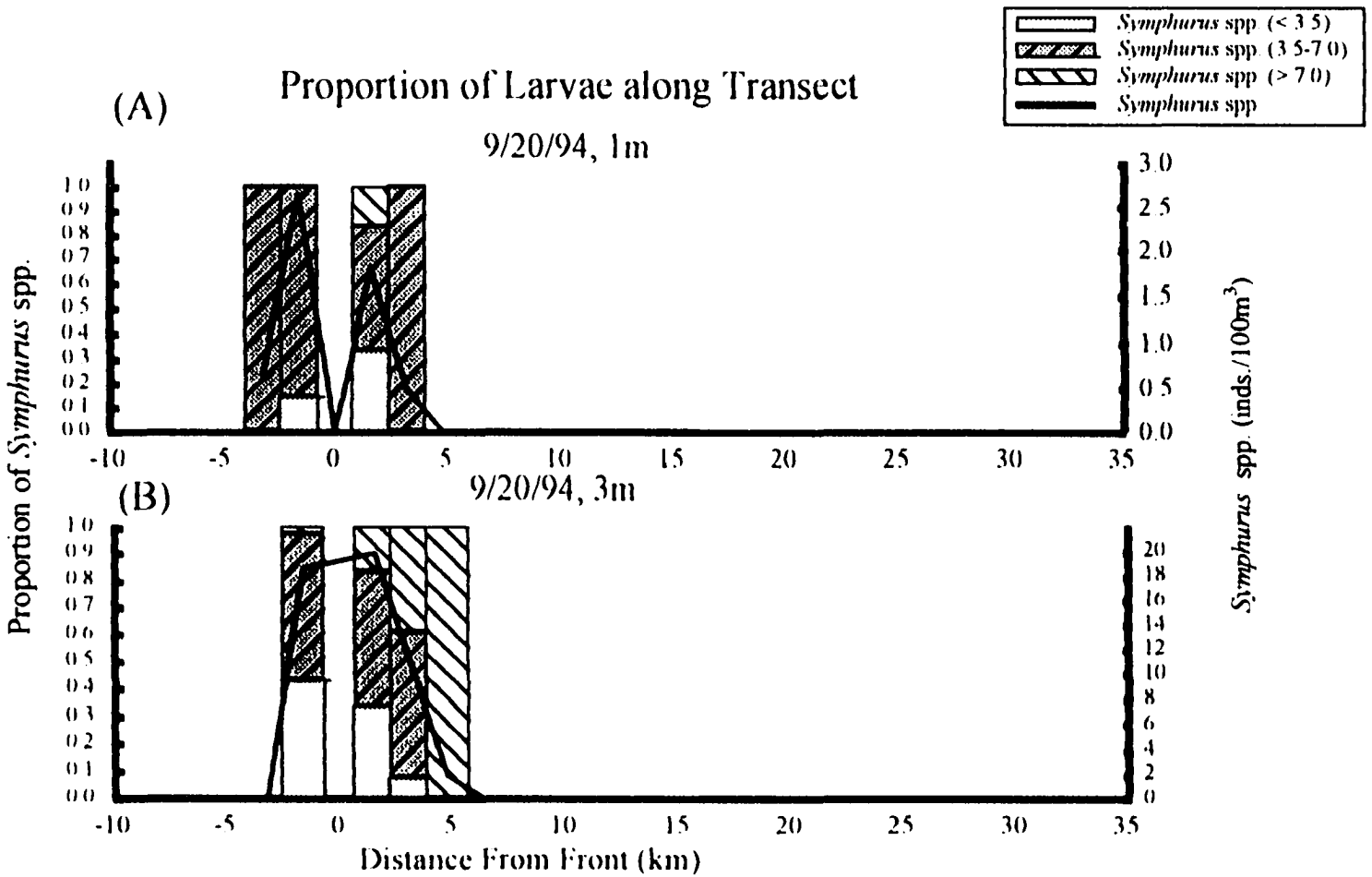

Figure 23 Proportion of ontogenetic stages (bars) and density (#/100m^3) of *Symphurus* spp along the transect on September 20, 1994 (a) 1m, (b) 3m

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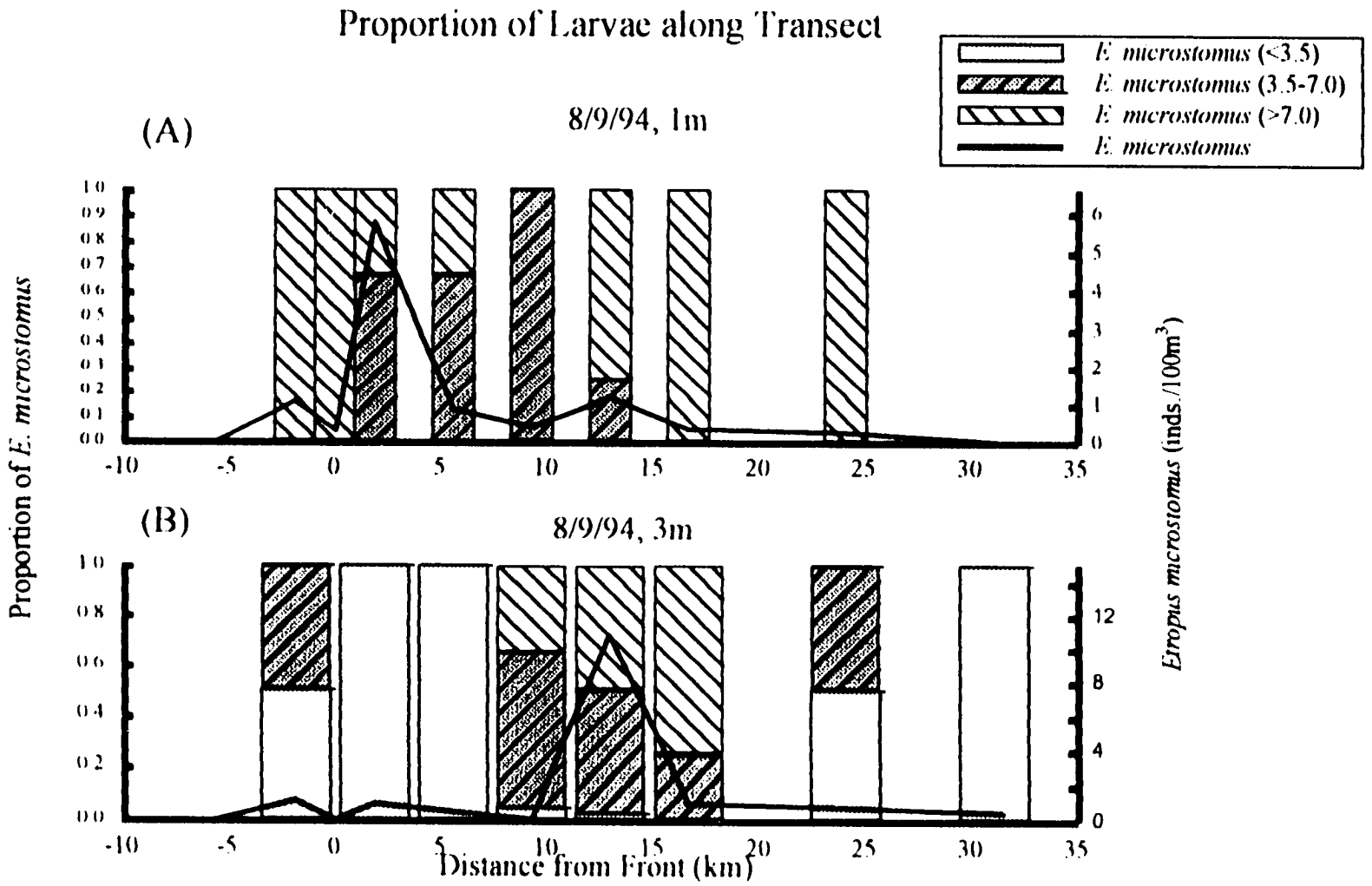

Figure 24 Proportion of ontogenetic stages (bars) and density (#/100m^3) of *E. microstomus* along the transect on August 9, 1994 (a) 1m, (b) 3m

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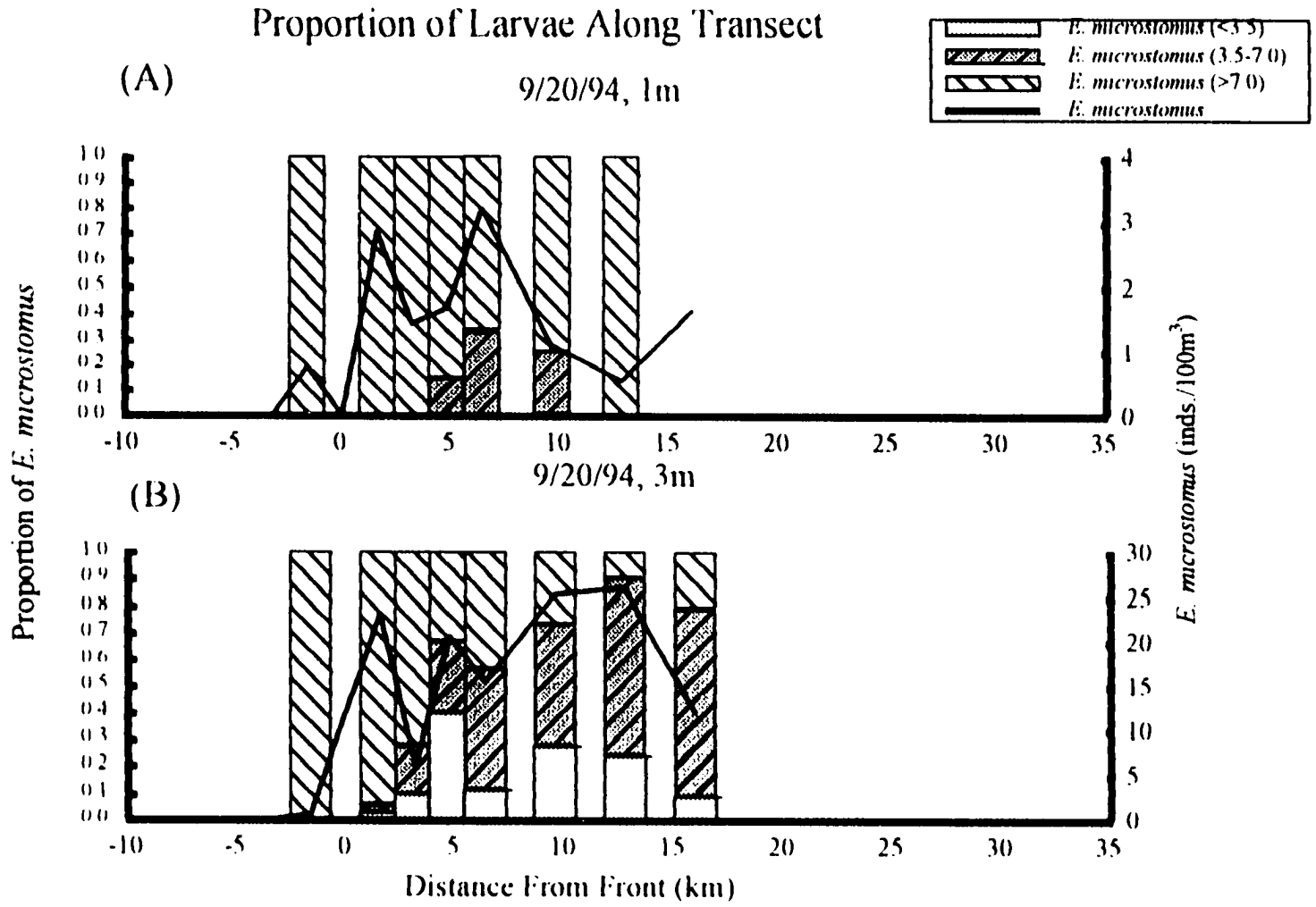

Figure 25 Proportion of ontogenetic stages (bars) and density (#/100m^3) of *E. microstomus* along the transect on September 20, 1994 (a) 1m, (b) 3m

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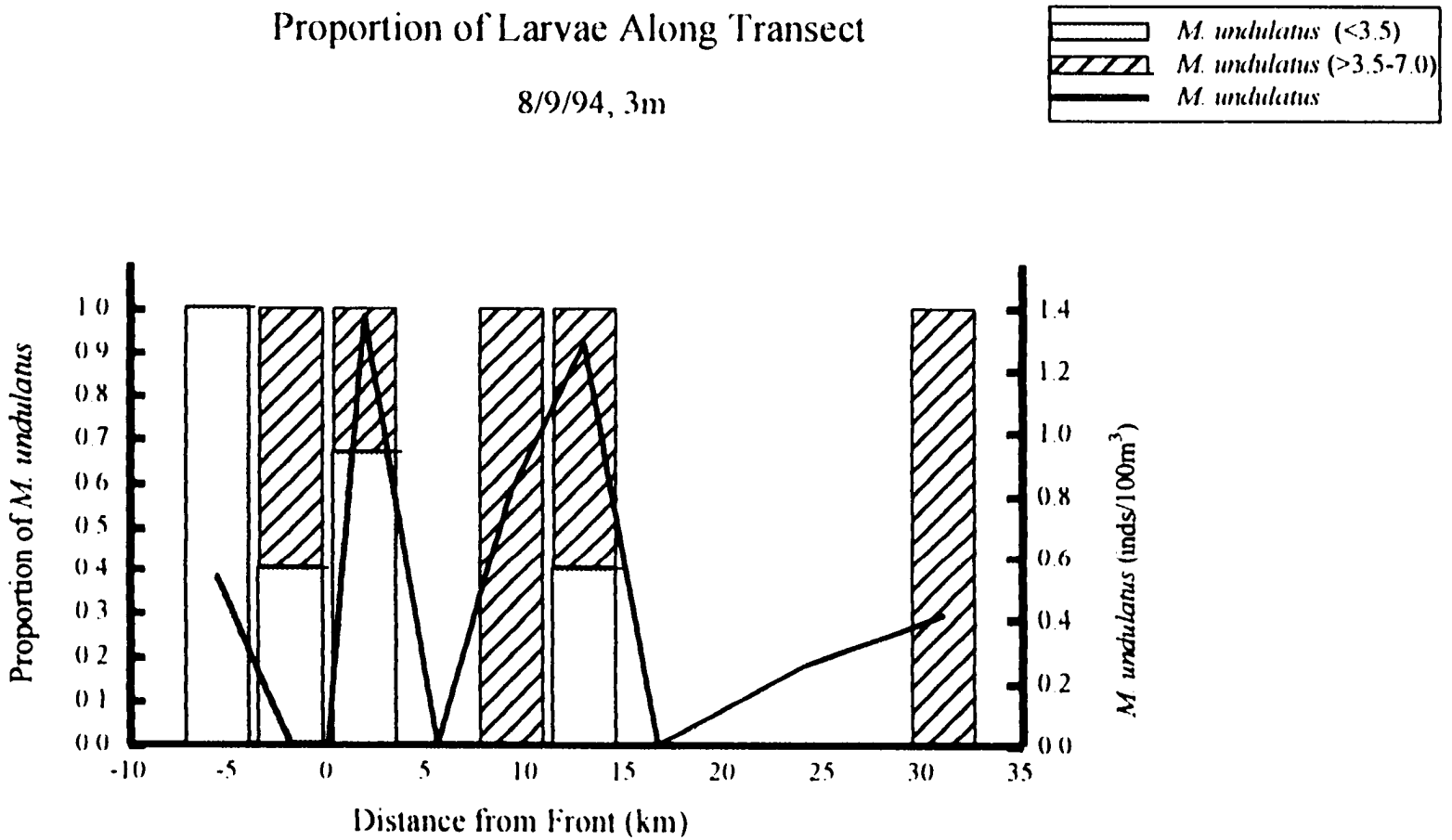

Figure 26 Proportion of ontogenetic stages (bars) and density (#/100m^3) of *M. undulatus* along the transect on August 9, 1994 at 3m

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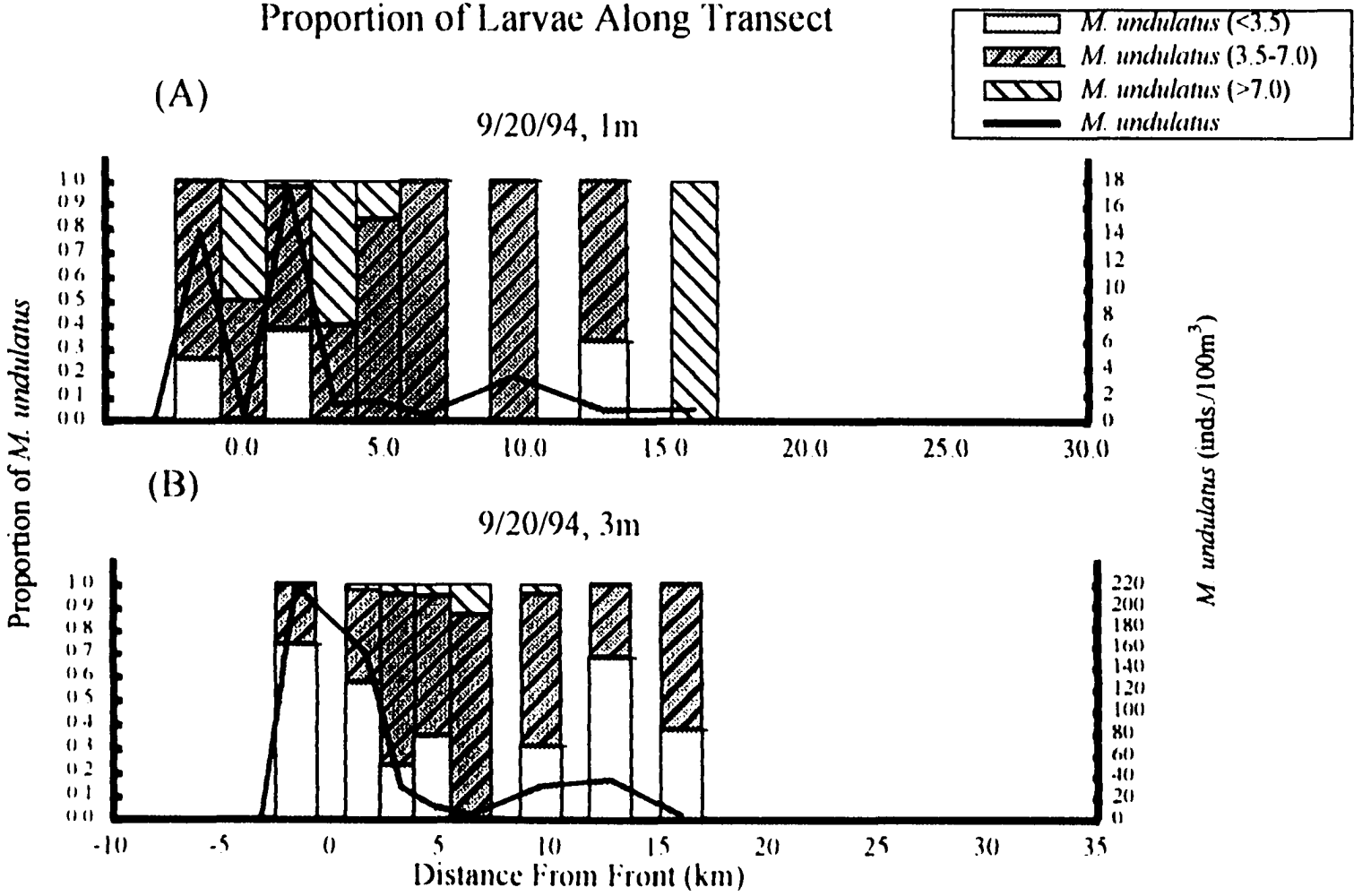

Figure 27 Proportion of ontogenetic stages (bars) and density (#/100m^3) of *M. undulatus* along the transect on September 20, 1994 (a) 1m, (b) 3m

exclusively seaward of the front. A similar ontogenetic pattern was found on September 20, with most larger larvae occurring offshore of the plume at both depths (Fig. 23 a, b). This pattern suggests that *Symphurus* spp. larvae were not retained within the plume by the front.

Etropus microstomus larvae were most abundant within shelf waters on all dates. The peaks in larval abundance on August 9 and September 20 were associated with intermediate and large larvae at both 1 and 3 m (Figs. 24-25). On August 9, the largest peak in abundance occurred just offshore of the front and was composed of intermediate and large larvae, at 1m (Fig. 24a). At 3m larval peaks were found about 12 km seaward of the front and consisted of larvae >3.5 mm in length. On September 20, the cross-frontal distribution of *E. microstomus* showed an increasing trend in abundance offshore. The cross-shelf pattern of some ontogenetic stages followed this trend, large larvae were found in the vicinity of the front, while increasing numbers of small and intermediate sized larvae were found offshore of the front in both 1m and 3m samples (Fig. 25 a, b).

The cross-shelf distribution of ontogenetic stages of *M. undulatus* differed from the pattern exhibited by *E. microstomus*. On August 9, small (<3.5 mm) larvae dominated in the vicinity of the front, while large larvae (>7.0 mm) were not captured at either 1 or 3m. Peaks in abundance offshore were dominated by intermediate sized larvae, at 3m (Fig. 26). On September 20, small and intermediate sized larvae were also most abundant at stations just inshore and offshore of the front (Fig. 27). Large larvae (>7.0 mm) were found mostly offshore of the front, but comprised a very low percentage of the total number of larvae captured.

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Discussion

The Chesapeake Bay plume front influenced the cross-frontal distributions of both indicator taxa, *E. microstomus* and *Anchoa* spp. These two taxa showed consistent differences as to which side of the front they occurred. This indicates that the plume front is an important feature in coastal and inner shelf waters for these taxa. Within Chesapeake Bay, Olney (1996) suggested that plume larvae were redistributed over the shelf as a consequence of mixing processes. The results of the current study show that mixing between zones was not common. Rather, delineation of assemblages as represented by *Anchoa* sp. and *E. microstomus* by the plume front was the consistent feature, even during upwelling when the plume front was located offshore.

Peaks in total larval density and for the taxa examined in this study (*Anchoa* spp., *M. undulatus*, *E. microstomus* and *Symphurus* spp.) occurred at stations inshore and seaward of the front, with no aggregation at the front itself. Additionally, the front was always visible as a flotsam line, with buoyant debris aggregated at the front. Accumulations of zooplankton were also visible as swarms or patches at the front (Reiss pers. obs.). The lack of aggregation of larval fish at the front is unexpected considering that many studies have found increased abundances of ichthyoplankton at fronts (Kingsford and Choat 1986, Govoni *et al.* 1989, Govoni and Grimes 1992, Grimes and Finucane 1991, Kingsford and Suthers 1994). The distance from the front to the larval peaks was usually more than 1 km. This distance is too far to reflect downwelling of buoyant larvae at the front and then re-surfacing of larvae. Another mechanism must be responsible for the observed multi-specific peaks inshore and offshore of the front.

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The influence of both the periodic nature of tides and the offshore movement of frontal zones has also been suggested as a mechanism for frontal aggregation in a variety of environments ranging from shelf waters (Sabates 1990) and tidal inlets (Dustan and Pickney 1989; Rothlisberg *et al.* 1989; Wheless 1993, Thorrold *et al.* 1993) to seasonal river plumes (Kingsford and Suthers 1994; Thorrold and MacKinnon 1995). Tidal currents cause the Chesapeake Bay plume front to strengthen and weaken with daily tides. The plume front migrates several kilometers across the shelf during each tidal cycle (Valle-Levinson, pers. comm.). Tidal currents are strong enough to mix the shallow water seaward of the front creating a water mass of uniform properties (temperature, salinity, and density) between the plume and shelf waters (Fig. 14, 15, 16) (Wiseman and Garvine 1995). This cyclic motion could sweep young and recently spawned larvae of coastal, shelf and translocated plume taxa back and forth across the inner-shelf. This could create the observed multi-specific peaks several kilometers on either side of the front. Additionally, this mixed water may have a higher residence time on the inner shelf, and larvae might be retained close to the baymouth by this mechanism.

There are however, several reasons that may explain the lack of aggregation at the front itself. First, the front is dynamic and ephemeral both tidally and over short time scales (days). Since sampling only occurred four days over the summer, the sampling may have temporally missed an aggregation event (at either tidal or daily period) (Govoni *et al.* 1989; Grimes and Finucane 1991). Second, the aggregated larvae may not have been sampled because they were transported laterally along the front similar to the transport of chl-a described by Dustan and Pickney (1989). Since this study examined only one transect near the baymouth, aggregated larvae may not have been sampled. Third, the

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larvae of taxa examined during this study were significantly more abundant at 3m depth on most occasions, indicating that these larvae are not neustonic or surface seeking, therefore frontal convergence may not have acted upon them directly (Olson and Backus 1985, Govoni *et al.* 1989; Govoni and Grimes 1992). Finally, there may be no aggregation occurring at the front and therefore the Chesapeake Bay plume front may not function in the same manner as other fronts (Grimes and Finucane 1991, Kiorboe *et al.* 1988). Instead the plume front may simply delimit the plume and shelf assemblages.

The cross-frontal pattern of ontogenetic stages of *Symphurus* spp. larvae during the current study suggests an ontogenetic migration from the plume to the shelf. A similar ontogenetic pattern of smaller larvae within the plume and larger larvae offshore was found off the baymouth by Reiss (chap. 2). The current results show that the ontogenetic pattern is consistent throughout the summer. This ontogenetic migration explains why *Symphurus* spp. was not strongly correlated with environmental parameters on individual sampling dates.

Densities of the two shelf spawned taxa, *E. microstomus* and *M. undulatus*, were positively correlated with each other for the summer but were not necessarily correlated on individual sampling dates. These two taxa have been classified together in the same shelf assemblage (Olney 1996) suggesting that they have the same general spawning distribution. The abundance and spatial distribution of small *M. undulatus* larvae within the frontal zone differed from the spatial distribution of small *E. microstomus*. Since larval distributions of early stages of these two taxa did not overlap considerably, spatial distributions probably arose because they do not share the same shelf spawning locations.

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The higher densities of small *M. undulatus* in the vicinity of the plume front is consistent with several other studies that examined the spawning and larval distribution of this species. In the South Atlantic Bight (SAB), *M. undulatus* spawning is seasonal (winter and spring) and related to water temperature (at least 18 ^{0}C). Water of this temperature is generally found near the Gulf Stream front during the spawning season (Hettler 1981). Warlen (1982) found that small *M. undulatus* larvae were more abundant within frontal waters of the SAB as compared to elsewhere on the shelf. These data support the hypothesis that physical features like fronts may influence the spawning location and spatial distribution of *M. undulatus*. Outside the Chesapeake Bay mouth, water of at least 18 ^{0}C was found beginning in early August (Fig. 11) and persists through October (Norcross and Austin 1988). Since water of appropriate temperature is present so close to shore, adult *M. undulatus* need only migrate to near-coastal areas to find suitable spawning temperatures. Barbieri *et al.* (1993) examined ovaries of *M. undulatus* in Chesapeake Bay and found evidence of spawning as early as July within the bay, supporting the hypothesis of local spawning.

Other studies performed near the Chesapeake Bay mouth have shown patterns of sciaenid abundance consistent with this frontal spawning hypothesis (Olney 1996, Reiss and McConaugha 1997, in prep.). Olney documented influx of yolk-sac sciaenid larvae at an offshore site during wind reversals in late August, when *M. undulatus* spawn. While he was not able to confirm the identity of the yolk-sac larvae as *M. undulatus*, larger *M. undulatus* were collected at those same sites. Reiss and McConaugha (1997, in prep.) found that during a summer upwelling event, the mesoscale distribution of *M. undulatus* was correlated with *Anchoa* spp. and not with *E. microstomus*. Based upon this

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correlation and the length frequency distributions of *Anchoa* spp and *M. undulatus* at inshore and offshore sites, they argued that the cross-shelf pattern was consistent with nearshore spawning of *M. undulatus* larvae coupled with advective transport to the mid-shelf. Therefore, the hypothesis that *M. undulatus* spawn in the vicinity of the front and are retained in the vicinity of the baymouth by tidal mixing and oscillation of the front is supported by the data of this study. To recruit to the bay, changes vertical distribution during ontogeny would provide a mechanism to transport larvae into the Chesapeake Bay via the sub-surface estuarine inflow (Norcross 1983, 1991, Weinstein *et al* 1980, Olney 1996).

The Chesapeake Bay plume front exhibited two major "modes" during this study and these were important in controlling the spatial distribution of ichthyoplankton. The first was a highly stratified "mode" (July 5) where stratification dominated across the shelf. The second "mode" occurred when the plume was compressed against the coast and waters seaward of the front were well mixed.

The stratified mode probably reflects coastal upwelling that forced the Chesapeake Bay plume seaward (see chap. 5). When this occurs sub-surface water is drawn to the coast from offshore (Hicks and Miller 1980, Reiss chap. 5). This combination of offshore transport at the surface and inshore transport at depth enhances stratification on the shelf. As a result high salinity shelf water enters the bay below the pycnocline. Shelf-spawned, estuarine-dependent could be advected into the bay-mouth during these events without complex larval behavior.

Predicting when offshore transport of the plume is likely to occur would be important if upwelling drives larvae into the bay. Kourafalou *et al* (1996a, 1996b) used

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the Richardson number, the ratio between buoyancy and mixing to characterize the stability of the SAB coastal zone to cross-frontal breaching. They were able to determine when meteorological conditions for cross-shelf breaching of the coastal plume would be likely. Since high bulk stratification is indicative of increased buoyancy, it may be possible to use a similar formulation to estimate the frequency and intensity of these offshore advection events within the Virginia shelf.

On all remaining cruises (August and September) the second mode dominated waters seaward of the front were relatively well mixed and exhibited low bulk stratification. This mode is consistent with downwelling favorable winds that compress the plume against the coast (Boicourt *et al.* 1987). In addition, the low bulk stratification on the shelf is consistent with tidal mixing over the shallow areas of the inner shelf. Olney (1996) found that waters in his offshore sites (approximately 25 km along this transect) were relatively well mixed except when winds transported plume water across the shelf in the surface. The mixed water observed seaward of the front may have a higher residence time on the inner shelf. If larvae are retained near the baymouth in this water mass, simple vertical changes in larval distribution could result in successful recruitment of estuarine-dependent taxa, like *M. undulatus*.

The plume is a dominant structuring force on the Inner Continental Shelf near the Chesapeake Bay Mouth. The plume and its associated front affects the cross-shelf spatial distribution of taxa during both upwelling and downwelling favorable conditions. The patterns of larval *Anchoa* spp. suggest that retention within the plume occurred for some members of the plume assemblage. The presence of large numbers of *M. undulatus* larvae in the vicinity of the baymouth as early as August 9 indicates that this taxa spawns during

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summer and contrasts with the current spawning and transport paradigms described by Norcross (1983,1991). By spawning near the plume front in coastal waters, *M. undulatus* may be retained in an area where tidal mixing retain larvae in the baymouth. At least one taxa, *Symphurus* spp., showed evidence of switching from within the plume to shelf waters with ontogeny. This result indicates the presence of ontogenetic behaviors by some taxa that will result in changes in assemblage membership. These data show that the physical dynamics associated with the Chesapeake Bay outflow are important factors in the distribution of ichthyoplankton on the inner shelf off of Virginia.

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CHAPTER 4

Small-scale cross-frontal distribution of ichthyoplankton across the Chesapeake Bay mouth

Introduction

Recruitment through inlets by estuarine-dependent larvae is thought to be determined by two processes: advective transport and concentration of larvae in the nearshore and then behaviorally mediated transport through the inlet (Weinstein *et al.* 1980, Boehlert and Munday 1988, Kingsford 1990). The supply of larvae to the nearshore is generally a passive process dominated by advection from offshore, but may result from local spawning in the coastal zone (Miller *et al.* 1982, Cowen *et al.* 1993, Govoni and Pietrafesa 1994). Recruitment into the estuary from nearshore can occur passively, by local meteorological forcing or may result from larval behaviors that enhance recruitment by using tidal currents, or residual estuarine circulation (Harden-Jones 1968, Weinstein *et al.* 1980, McLeave *et al.* 1984, Norcross 1983, Norcross and Shaw 1984, Norcross 1991).

Within estuaries, tidal and baroclinic processes setup fronts that can enhance retention or may create physical barriers to transport (Epifanio 1987, Sinclair 1988, and Taggart *et al.* 1989). In Chesapeake Bay, fronts form and dissipate at tidal frequencies, recur in the same locations, and separate mixed waters over the shoals from rapidly flowing water within the channels (Simpson and James 1986, Valle-Levinson and Lwiza

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1996). These physical features may concentrate predator and prey or may enhance encounter rates on shoals or at fronts (Rothschild and Osborn 1987, Govoni and Olney 1991). One study in Chesapeake Bay has found that potential predation of fish eggs by medusae may be greater over mixed waters (on shoals) compared to stratified waters (in channels) within the Chesapeake Bay mouth. Fronts and shoals within the estuary may then influence survival of larval fish (Govoni and Olney 1991).

This study examines the abundance and vertical distribution of ichthyoplankton across an estuarine front in the mouth of Chesapeake Bay. The primary goals were to determine whether larvae were aggregated within the front, and whether the small scale distribution of inshore and offshore spawned larvae is affected by the position of the outflow plume. Spatial distribution and abundance of total ichthyoplankton, *Anchoa* spp., *Symphurus* spp., and *M. undulatus* were related to cross-frontal density patterns. Abundances were compared between three zones, plume (1-3m), channel (>3m) and shoals (1-5m) representing three hydrographic conditions, estuarine outflow (the plume), inflow (within channels at depth), and mixed waters (shoals).

Oceanography of the Baymouth

The Chesapeake Baymouth is dominated by a complex of shoals and channels that provide considerable topographic steering of the inflow and outflow of the bay. Three channels >20 m in depth are almost equally spaced across baymouth. These channels are interrupted by shoals <10 m deep. A considerable horizontal difference in both density and currents occurs across the wide (17 km) baymouth. As a result of the Coriolis force net outflow is concentrated at the surface on the south side of the bay. Additionally, net inflow occurs in the channels while outflow can occur over the shoals. The complex of

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channels and shoals creates a series of sheer fronts between each of the channels (LaCouture 1983 after Oertel). The fronts arise from shear between fast moving water within the channels and slower water moving over the shoals (Valle-Levinson pers comm.) as well as density differences resulting from the outflow of estuarine water at the surface. The water over the shoals may have a longer residence time within the baymouth compared to water in the channels (Valle-Levinson pers comm) This increased residence time could therefore influence survival of larvae that are spawned over or transported onto the shoals, by retaining them within the baymouth.

Methods and Materials

Ichthyoplankton samples were collected during a cruise from August 27-28, 1992. A single transect consisting of 7 stations was sampled across a front located in the mouth of the Chesapeake Bay. The location of the transect was in an area of known frontal formation (LaCouture 1983 after Oertel), and is composed of a channel and a shoal complex (Fig. 28). Stations along the transect were located at 1 km intervals and during daylight, a station was sampled directly in the front. Samples were collected continuously over a 24 hour period. Over the channel, where water depths exceeded 10m, samples were collected at 1, 3, 7, 9m, while over shoals samples were collected at 1, 3 and at times 5 m

Ichthyoplankton samples were collected using a 75-cm opening and closing bongo net fitted with 333μ Nitex mesh and General Oceanics model 2030 mechanical flowmeters. Plankton were stored in 10% formalin and later transferred to 70% ethanol for preservation. All ichthyoplankton were identified to the lowest possible taxon and densities are reported as #/100m^3. Before and after each transect, a CTD was used to

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measure environmental parameters at the 7 stations along the transect Salinity and density were derived from the measured properties of the CTD Each hydrographic transect took approximately 25 minutes to complete, while biological transects took approximately 5 hours. A total of four biological and five hydrographic transects were completed over the 24 hr period.

Sections of density were plotted for each transect, to determine the position of the front and to examine the density structure over the shoals In addition, bulk stratification ((bottom density - surface density)/depth) was calculated to determine the relative stability of the water column. Sections were also compiled for total ichthyoplankton, *Anchoa* spp., *Micropogonias undulatus*, and *Symphurus* spp Kruskal-Wallis non-parametric ANOVA was used to compare larval abundance between the plume (<5m), the shoals (stations 5, 6 and 7) and inflowing sub-surface waters (> 5m).

Results

Hydrography and physical oceanography

Strong fronts were associated with a plume of low density water that varied in position from the mid-channel to the shoals over the course of the study (Fig 29a-e) Density contours revealed that the position and strength of the associated front reflected ebb and flood tides. On flood tide transects, low density water was confined to the SW portion of the transect, while on ebb-tides low density water extended further NE Over the shoals, the water column was mixed with little vertical stratification, regardless of tidal stage. This water was relatively high in density (> 19 σ-t) owing to higher salinity coastal water that was mixed with it. On all transects except transect 3 bulk stratification was

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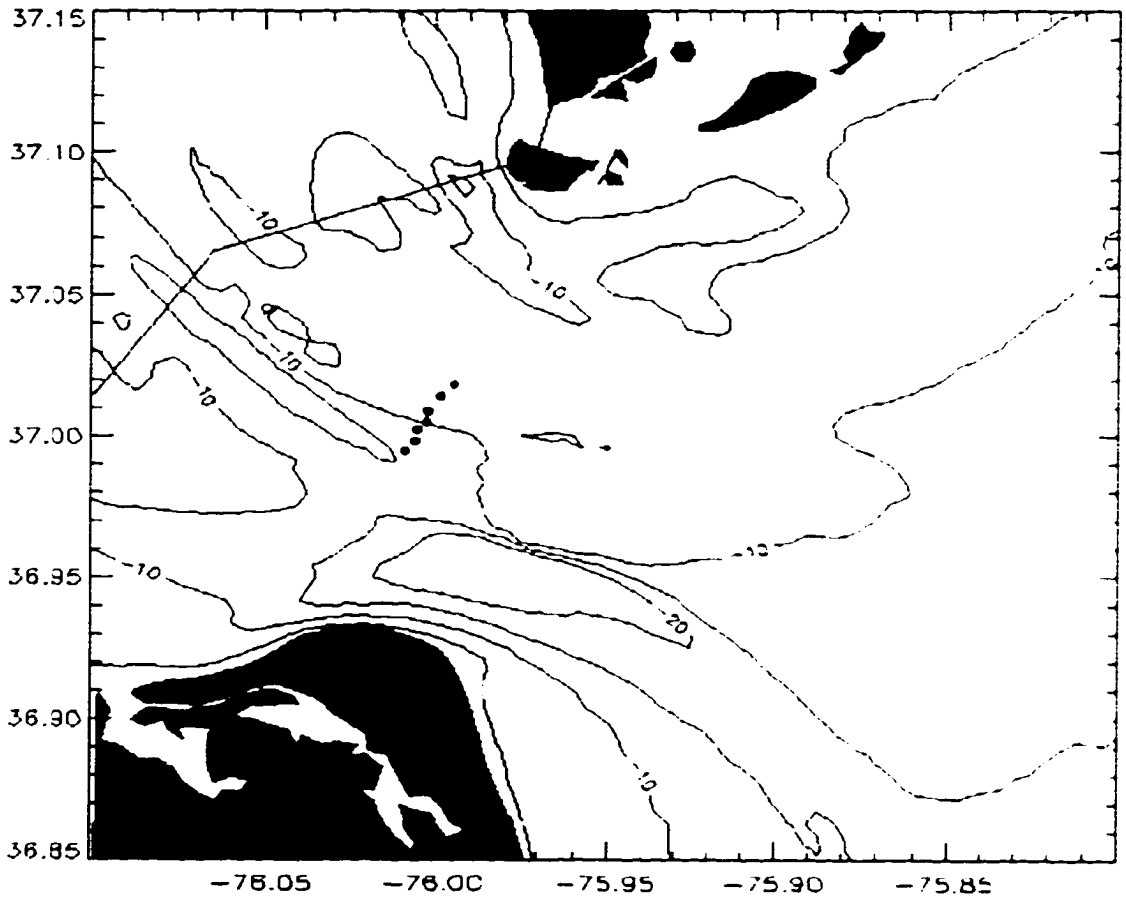

Figure 28. Map of sampling stations during cruise within the Chesapeake Bay mouth. August 27-28, 1992.

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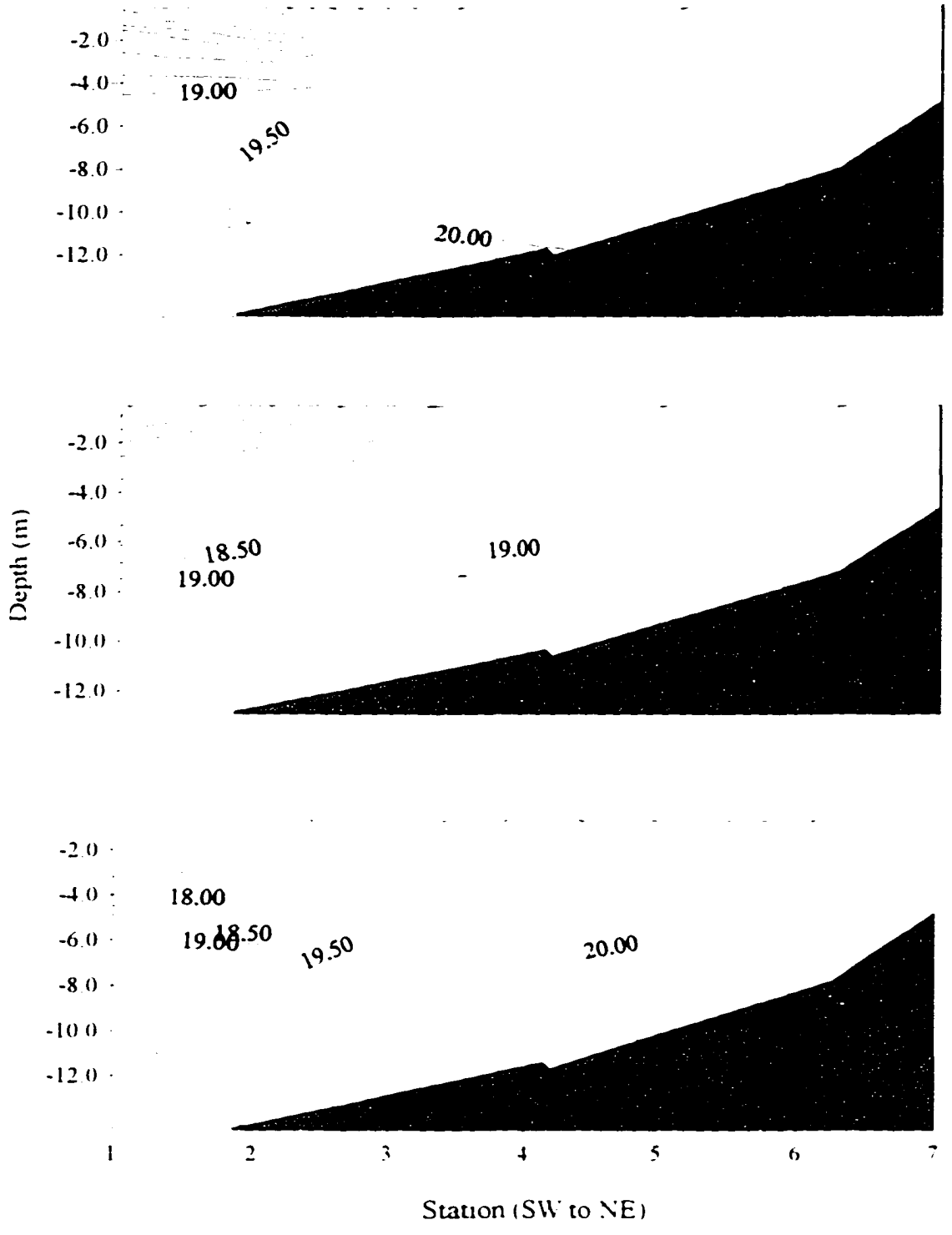

Figure 29 Contour plots of density (σ-t) across front on August 27-28, 1992. (A) Flood tide transect 1, daylight, August 27. (B) Ebb tide transect 2, daylight August 27. (C) Flood tide transect 3, nighttime August 27. (D) Ebb tide transect 4, nighttime, August 28. (E) Flood tide transect 5, morning August 28

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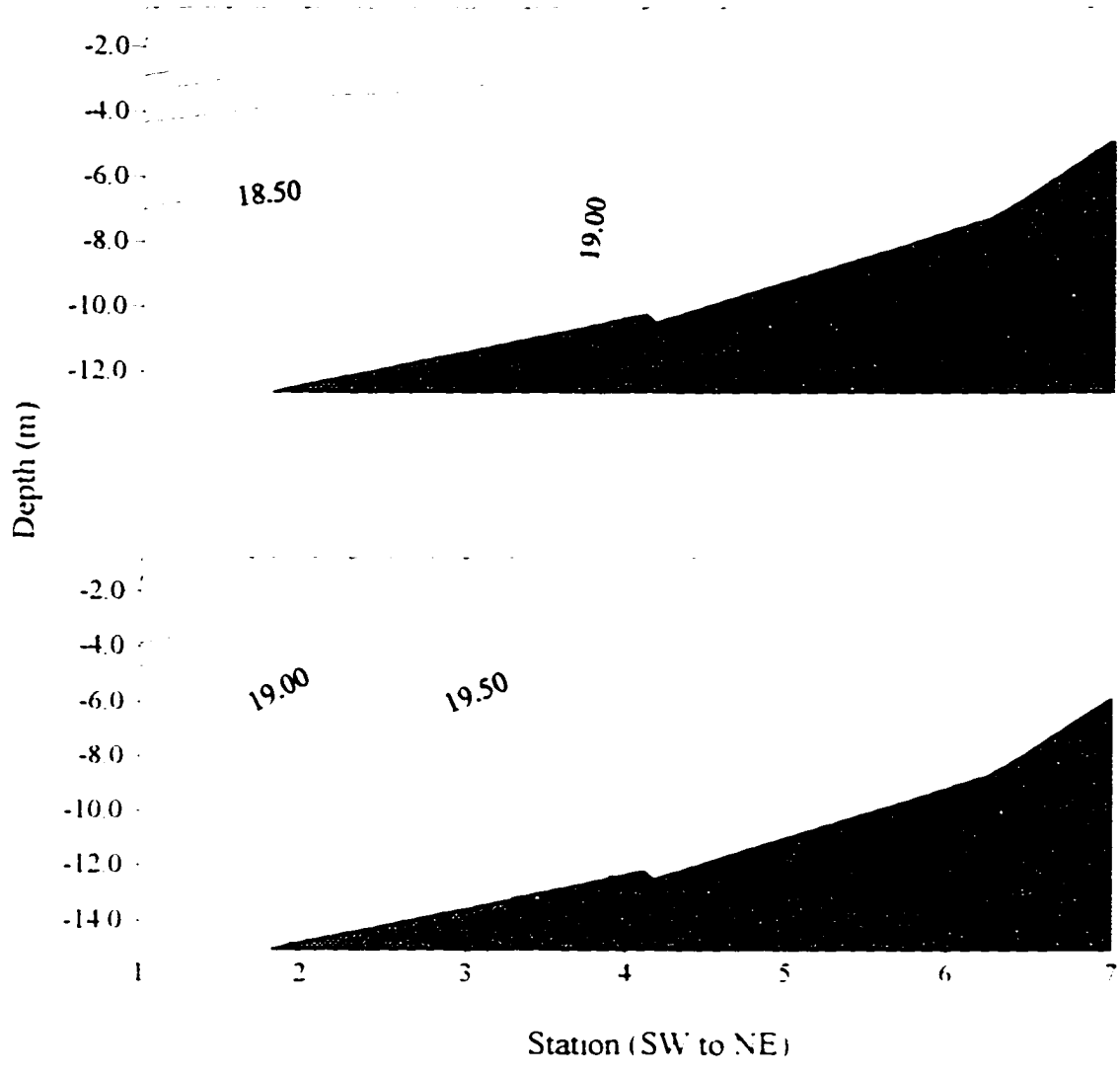

Figure 29 - continued

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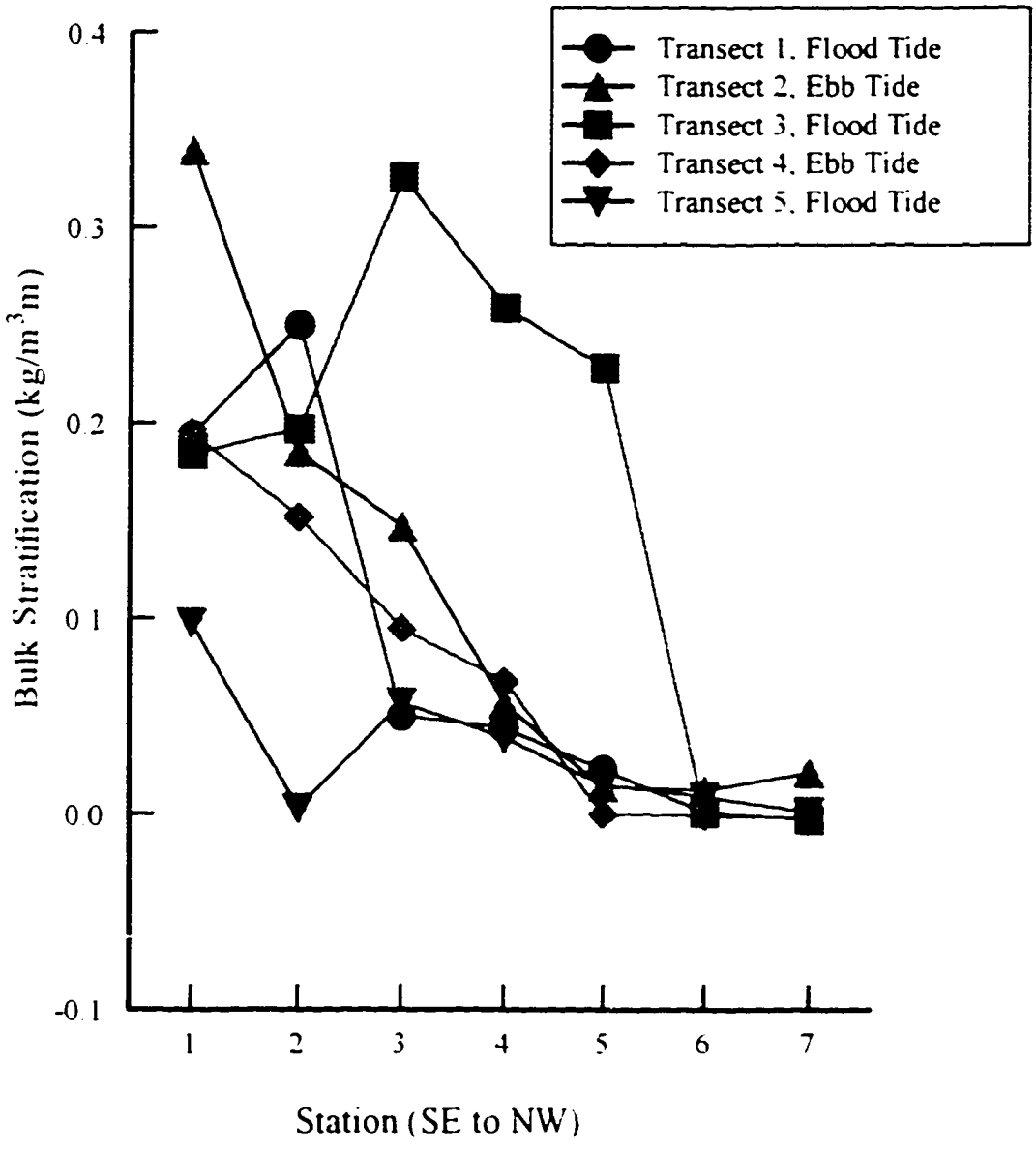

Figure 30 Plot of bulk stratification ($kg/m^3/m$) across the transect on five transits, August 27-28, 1992

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highest over the channel (stations 1 and 2), and decreased across the transect approaching zero over the shoals (stations 6 and 7) (Fig. 30).

Ichthyoplankton abundance and distribution

Fifteen taxa of ichthyoplankton representing 13 families were collected during this cruise (Table 12). Combining all samples, six taxa had mean overall densities that exceeded 1.0/100m^3. Three taxa, *Anchoa* spp., Blenniidae, and *M. undulatus*, had mean overall densities greater than 5.0/100m^3. Taxa common in shelf waters like *Etropus microstomus*, *Prionotus* spp., and *Ophidion* spp. were rare and comprised <0.01% of all larvae collected during this cruise.

The spatial distribution of total larval abundance reflected the density distribution across the sampling transect, and no aggregation was evident within the frontal zone (Fig. 31). Overall larval abundance was significantly different between zones (Table 13) and was always lowest within the plume. Maximum larval densities occurred below three meters and over the shoals, but these larval peaks differed between transects. In particular, on the third transect when the water column was highly stratified, larval densities were greatest at depth and decreased from the southwest to the northeast. The spatial distribution of larvae seemed to reflect the physics of the plume on each transect.

The cross-frontal distribution of *Anchoa* spp. followed the general pattern for total larvae (Fig. 32). Larvae of this taxa did not show a strong affinity for the surface plume and were found just below the plume at the depth of the pycnocline (Fig. 32). Additionally, larvae of *Anchoa* spp. were found over the shoals where the water column was mixed, especially on ebb tides. On flood tides larval *Anchoa* spp. were more concentrated over the channel, and this suggests that these larvae may respond to tidal

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Table 12. Overall mean density of ichthyoplankton collected in the Chesapeake Bay mouth, August 27-28, 1992. Larval densities from four transects were combined and averaged (n=45).

Variables	Mean	Std. Deviation	Maximum
Anchoa spp.	6.2	9 55	42 3
Blenniidae	5 67	16 09	83 75
Micropogonias undulatus	5 35	15 54	89 5
Gobiidae	2 79	6 77	41 04
Hippocampus erectus	1 67	8 69	58
Symphurus spp.	1 61	2 56	12
Trinectes maculatus	0 52	0 79	3 22
Syngnathus fuscus	0 13	0 29	1 33
Prionotus spp.	0 11	0 31	1 86
Menticirrhus spp	0 06	0 24	1 43
Gobieoscidae	0 02	0 1	0 51
Etropus microstomus	0 01	0 09	0 62
Ophidion spp	0 01	0 09	0 62
Hemiramphidae	0 01	0 06	0 45
Astroscopus guttatus	0 01	0 06	0 41

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Table 13 Results of Kruskal-Wallis test across three zones (inflow, outflow and shoals (A) Total ichthyoplankton, (B) *Anchoa* spp., (C) *Symphurus* spp and (D) *Micropogonias undulatus*.

Method	DF	Chi-square (H)	Prob Level
Total Ichthyoplankton			
Corrected for Ties	2	7.535986	0.023098
Number Sets of Ties	2		
Multiplicity Factor	30		
***Anchoa* spp.**			
Corrected for Ties	2	4.747397	0.093136
Number Sets of Ties	5		
Multiplicity Factor	798		
***Symphurus* spp.**			
Corrected for Ties	2	0.1849156	0.911688
Number Sets of Ties	6		
Multiplicity Factor	1746		
Micropogonias undulatus			
Corrected for Ties	2	2.516887	0.284096
Number Sets of Ties	2		
Multiplicity Factor	5820		

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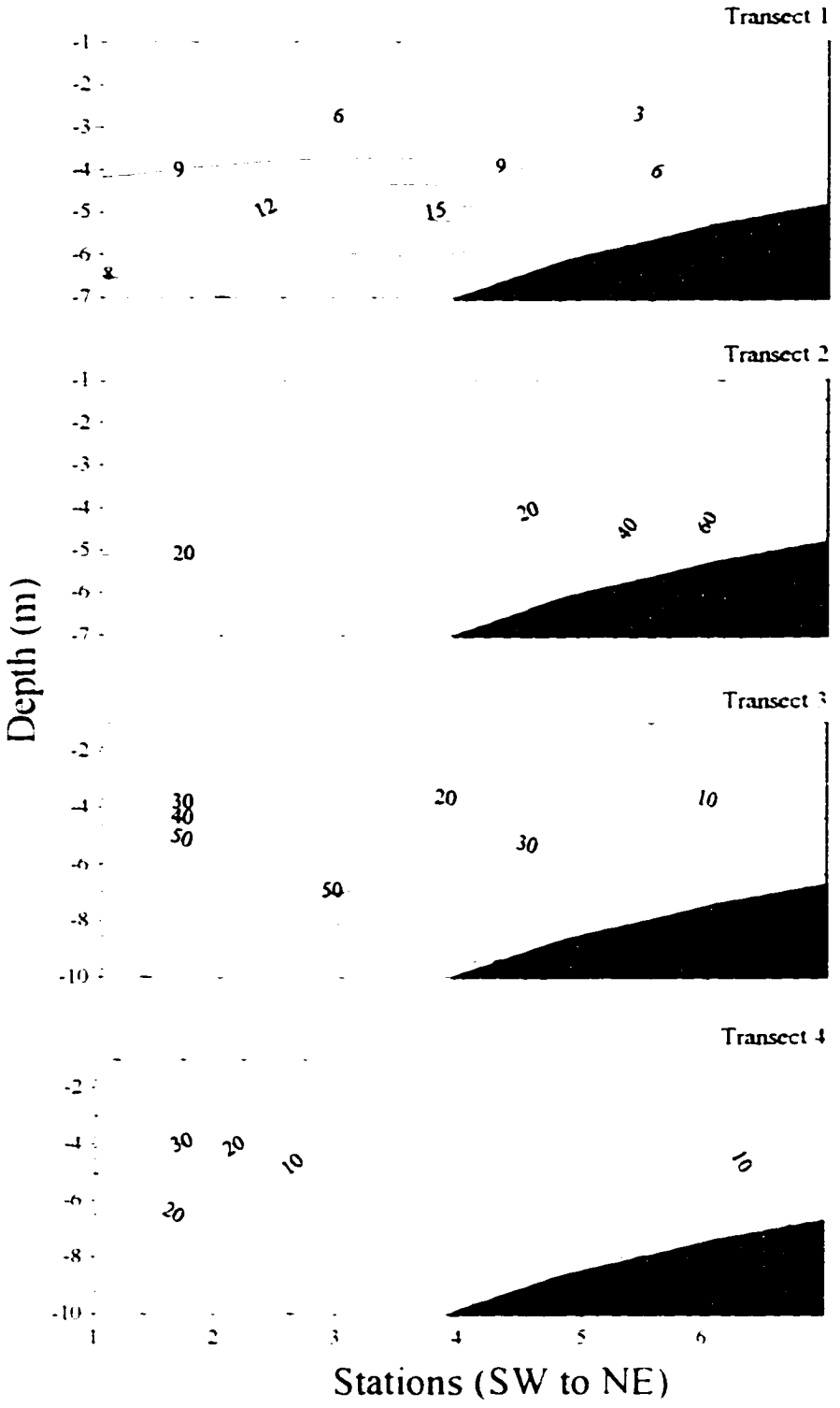

Figure 31 Cross frontal distribution of total ichthyoplankton (#/100m^3) across the four biological transects, August 27-28, 1992

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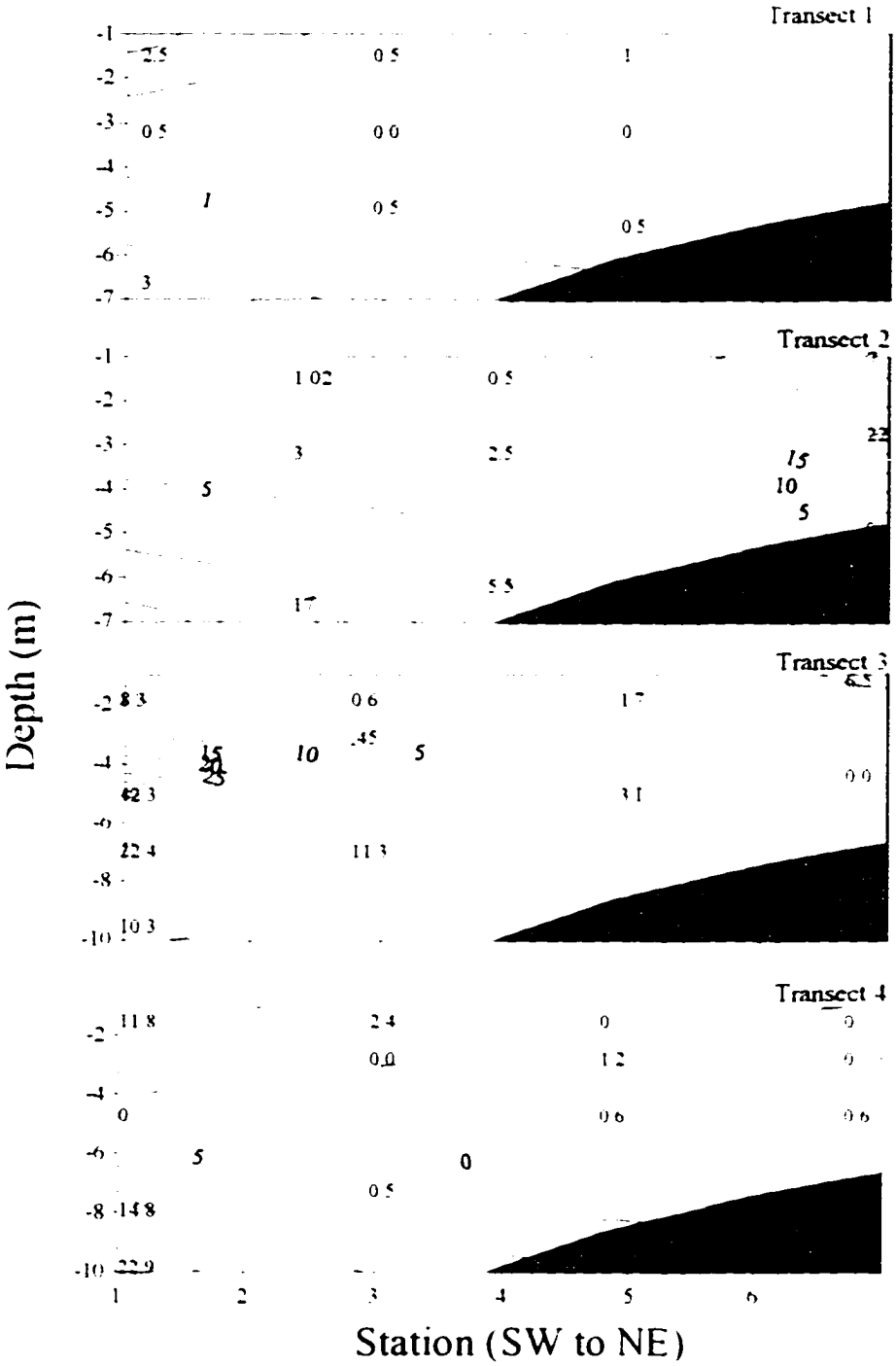

Figure 32 Cross-frontal distribution of *Anchoa* spp (#/100m^3) across each of the four biological transects, August 27-28, 1992 Data values for each smple are presented

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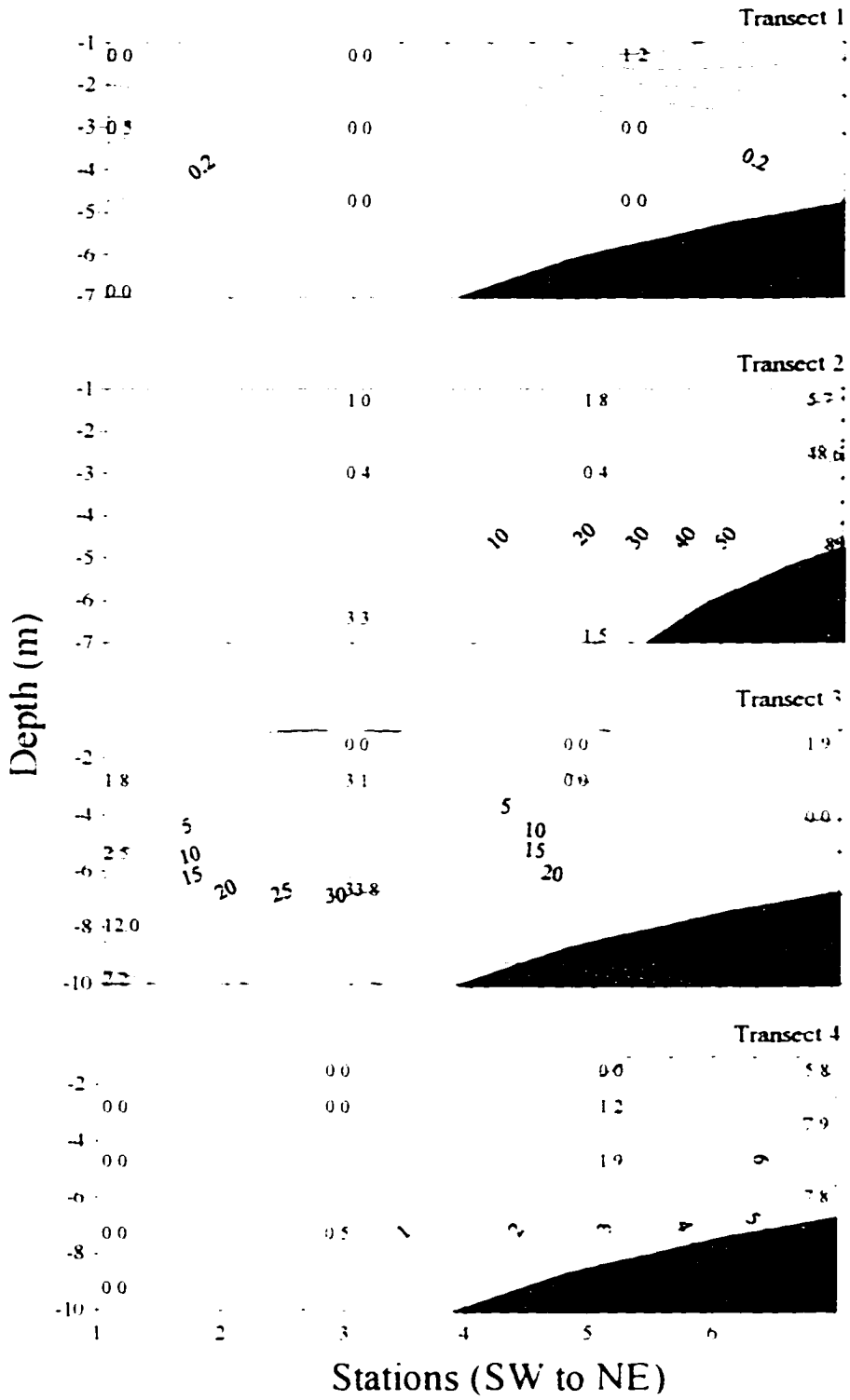

Figure 33 Cross frontal distribution of *M. undulatus* (#/100m^3) across each of the four biological transects, Aug 27-28, 1992 Data values for each sample are presented

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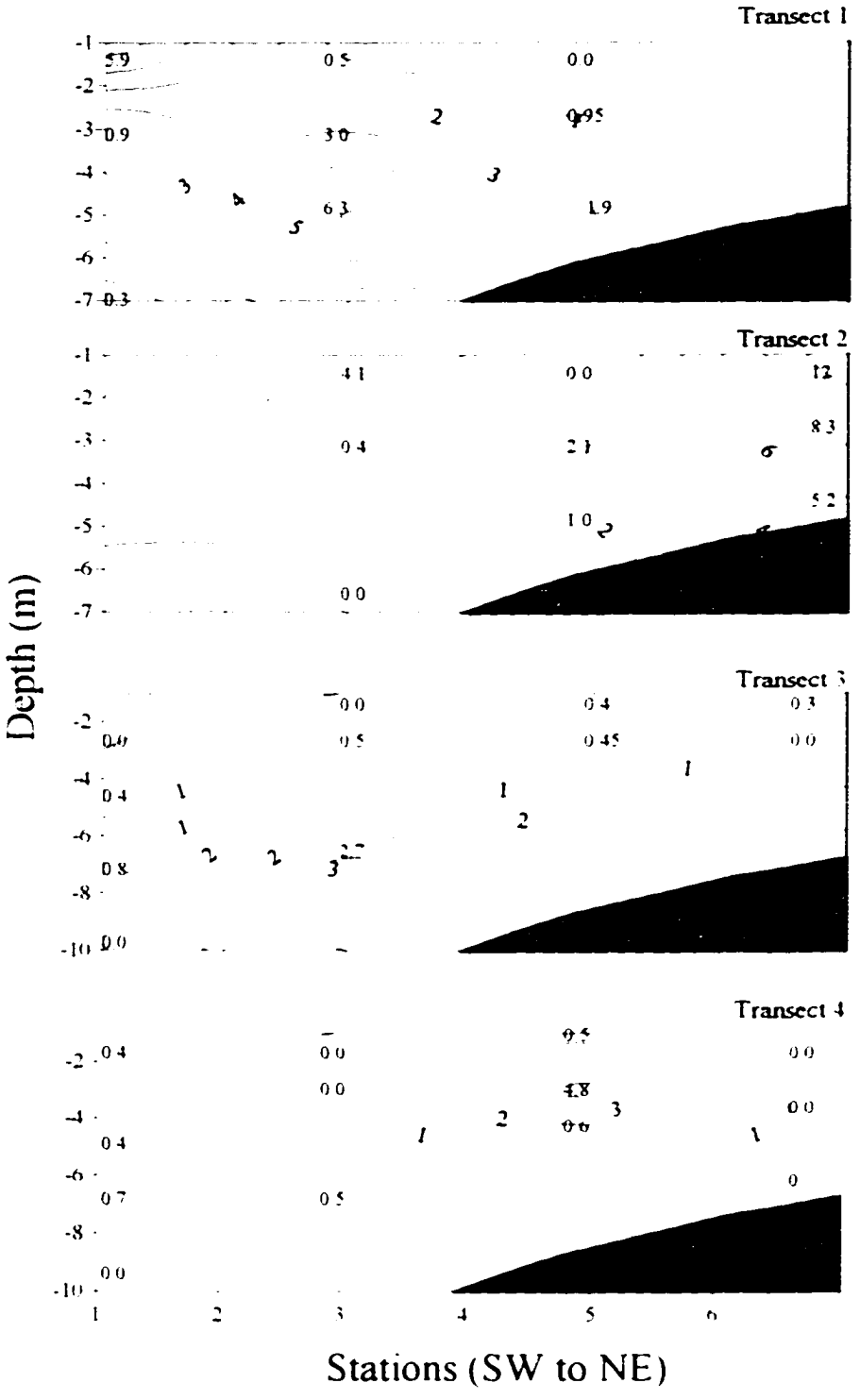

Figure 34 Cross frontal distribution of *Symphurus* spp (#/100m^3) across each of the four biological transects, Aug. 27-28, 1992 Data values for each sample are presented

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flows by moving into the water column on flood tides

The distribution and abundance of *M. undulatus* reflected the near coastal origin of this species, and consequently larvae were most abundant within the high density water of the channels and the shoals. When all transects were combined there was no significant difference in larval abundance between zones (Table 13). On individual transects however, the cross-frontal distribution clearly reflected the physics of the oscillating plume and its associated front. For example, during the third transect when the plume extended from the southwest almost to the shoal, larvae were concentrated at depth. On the second and fourth transects when there was no strong frontal gradient, larvae were more evenly dispersed in the high density water within the channels and over the shoals (Fig. 33).

The cross-frontal distribution of *Symphurus* spp. was more heterogeneous than for either *M. undulatus* or *Anchoa* spp., and did not reflect the density pattern in a way that was consistent with either plume or shelf sources (Fig. 34). This taxa did not show any significant difference between zones (Table 13) and instead reflected a patchy distribution characteristic of a taxa with low abundance.

Discussion

There was no evidence of aggregation of larvae, either overall or by species within the frontal zone. This pattern of low densities of larvae within a frontal zone has been shown for tidal fronts within estuaries and on the coast. Taggart *et al.* (1989) related this phenomenon to two factors, retention of larvae in different water masses separated by the front and increased predation within the frontal zone. Increased densities of larval predators were not found at the front, supporting a physical explanation for the lack of aggregation. The most plausible is that larvae were not neustonic so that they were not

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aggregated by convergent downwelling.

Despite the considerable temporal difference in the biological and physical sampling scales during this study, there was strong evidence that the physics of the plume affected the distribution of larvae and to a lesser extent larval assemblages within the baymouth. The density structure observed during the current study reflected the ebb and flood of the tides with low density water moving north across the sampling area during ebb. In general larval distributions reflected the source of the water where they developed, hence larvae were separated by the pycnocline in most cases. This indicates that larval assemblages retain there integrity into the baymouth.

Larvae from both the shelf and the plume co-occurred over the shoals, and this probably results from tidal mixing. Olney (1996) found a mixed assemblage that lacked distinct hydrographic or larval indicators. He believed that this mixed assemblage arose from mixing of plume and shelf waters, but did not give a mechanism for the mixing. At least one of his stations dominated by the mixed assemblage was located on a shoal within the baymouth. The results of this study suggest that tidal mixing over the shoals may explain the mixed assemblages he observed within the baymouth.

The channels within the baymouth are oriented perpendicular to the tidal currents so that inflowing or outflowing water generally flows around shoals not over them. As such, larvae that are spawned or transported onto the shoals may be retained against net outflow of the bay. Govoni and Olney (1991) found that potential predation rates were higher over shoals within the Chesapeake Bay mouth as compared to the stratified channels because predator and prey were mixed together (Govoni and Olney 1991). Whether larvae that are found on the shoals are retained within the baymouth, experience

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increased growth, or increased predation are important in considering whether these smaller scale fronts affect larval retention, recruitment and survival

Fifteen taxa were captured during this cruise as compared to over 30 taxa collected within the plume and inner shelf only one month before (Reiss chap 3) While this may be explained by the greater area sampled in that study, it may also reflect differential recruitment or differences in spawning location of estuarine-dependent taxa (Smith and Richardson 1977; Boehlert and Munday 1988, Lyczkowski-Schultz *et al* 1990; Warlen and Burke 1990; Raynie and Shaw 1994) There were few larvae of shelf-spawned shelf-dependent larvae like *E. microstomus*, *Prionotus* spp or *Ophidion* spp collected in the baymouth during this cruise despite the abundance of a shelf-spawned estuarine-dependent taxa, *M. undulatus*, that were captured Reiss (chap 2) found that the vertical distribution of *E. microstomus*, a shelf-spawned shelf-dependent taxa, varied dielly He suggested that such a difference would result in offshore retention against the net estuarine inflow on the shelf This may in part explain the lack of shelf-spawned shelf dependent taxa found within the baymouth during this study The abundance of *M. undulatus*, within the baymouth associated with higher density water suggests the potential for behaviorally mediated recruitment or local spawning of *M. undulatus* within the baymouth over physical transport during the current study

These data suggest that small-scale fronts within the Chesapeake Bay can affect the spatial distribution of larvae Differences in abundances between shoals and channels reflects the influx of larvae with the estuarine tidal flow Over shoals larvae of different spawning locations were mixed together suggesting that predator-prey and transport dynamics may be modified over such features Small scale features are strong determinants

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of the spatial structure of ichthyoplankton assemblages in estuaries where mixing should be higher

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CHAPTER 5

Distribution of ichthyoplankton in Virginia Shelf waters during summer upwelling

Introduction

Most marine fish have retained planktonic larval development as a part of their reproductive strategies. Due to the small size of planktonic larvae, both physical and biological mechanisms play an important role in determining recruitment success or failure (Rothschild 1986). A classic physical explanation for the fluctuations of fish populations has been attributed to transport of larvae away from favorable habitats (Hjort 1914), which may lead to increased starvation (Hjort 1914, Lasker 1975, 1978), or predation (Hunter 1981).

Mesoscale features such as fronts and eddies may be important for transport or retention of many coastal- or shelf-spawned, estuarine-dependent taxa (Richardson *et al.* 1980; Iles and Sinclair 1981, Boehlert and Munday 1988, Cowen *et al.* 1993, Govoni 1993). For example, frontal zones along continental shelf breaks or between major ocean currents are dominant features that can retain larvae or delineate spawning areas or transport routes (Nakata *et al.* 1989, Govoni 1993). On smaller scales, distinct differences in the ichthyoplankton assemblages associated with water properties inside and outside of estuarine or river plume boundaries have been found (Richardson *et al.* 1977, Sabates

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1990; Grimes and Finucane 1991). These findings indicate that physics can control the spatial distribution of ichthyoplankton and may affect survival of larvae within a spawning season (Sabates and Olivar 1996).

Position and strength of estuarine and riverine plumes are modified by variations in wind forcing and freshwater discharge (Garvine 1976, Boicourt 1981, 1987). Sabates (1990) and Thorrold and McKinnon (1995) showed that episodic meteorological conditions can affect the mesoscale spatial distribution and transport of larvae. Therefore, it is likely that wind induced coastal upwelling may affect the spatial distribution of fish larvae. If so, coherent movements of water to or away from the coast as a result of meteorological or oceanographic forcing may drive intra-seasonal recruitment events directly, through advection, or indirectly by altering the structure of the environment in which larvae develop.

Studies on the distribution of meroplankton in the continental shelf waters of Virginia are limited. Most studies have focused on the distribution of single groups of organisms with respect to spawning location and times (Norcross *et al.* 1974, Varnell 1989). Few others have tried to describe the assemblages, or groups of co-occurring taxa (Goy 1976; Maris 1986). Recently, two studies have demonstrated that plankton assemblages can be described by salinity and temperature signals characteristic of either bay or coastal waters (Seibel 1993, Olney 1996). Olney (1996) documented the presence of three ichthyoplankton assemblages within the plume and on the Inner-shelf. These assemblages included 1) an inshore low salinity (<29) plume assemblage, dominated by anchovy (*Anchoa* spp.), Gobiid and Blenniid larvae, 2) a high salinity (>32) shelf assemblage, dominated by Atlantic croaker (*Micropogonias undulatus*), tonguefish

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(*Symphurus* spp.) and cusk eels (*Ophidion* spp.), and 3) a mixture of the above two types. It may useful to examine how different taxa from the various assemblages are affected by meteorological forcing. For example, *Anchoa* spp. which is known to spawn within the Chesapeake Bay might be useful as an indicator of displacement of the plume assemblage. By examining its spatial distribution inferences regarding transport of the plume assemblage to the shelf can be made. Similar inferences on cross-shelf transport might be made using expatriate taxa like *X. novacula*, which is known to spawn in the South Atlantic Bight, and is transported north to the MAB by the Gulf Stream (Hare and Cowen 1991; Cowen *et al.* 1993). The distribution of other larvae whose spawning and spatial patterns are not well known may then be inferred relative to the distribution of other taxa, whose origins are known.

This study examines the spatial distribution of ichthyoplankton over the continental shelf during a period of upwelling. Two questions were addressed: (1) how are the local distributions of members of plume and shelf assemblages affected by wind induced coastal upwelling; (2) what is the relative role of mixing and advection in determining the distributions of ichthyoplankton across the frontal zone during this event? These questions were addressed by determining the spatial distribution of the plume and shelf assemblages, as well as expatriate taxa using multivariate analysis. The derived assemblages are then correlated with hydrographic and environmental parameters (temperature, salinity and chl-a), and the spatial pattern was related to the dynamics of coastal upwelling.

Oceanography of the Virginia Shelf

Virginia shelf waters are a mixture of water masses (Norcross and Harrison 1967). Three specific water masses are found on the Mid-Atlantic shelf off of Virginia. The first is

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Chesapeake Bay Plume water that has the lowest salinity (<30). The second water mass is Mid-Atlantic shelf water that has salinities between 32-34 and temperatures that vary seasonally (Manning 1991, Mountain 1991). During the summer, temperatures of this water mass range from about 18-22 ^{0}C. The third water mass is Mid-Atlantic Cold Pool water (CPW), a remnant of winter cooled shelf water, and is characterized by its low temperature (<10 degrees) rather than salinity (~33). CPW is found at depth near the shelf edge throughout the MAB (Houghton *et al.* 1982, Houghton and Marra 1983).

The Chesapeake Bay Plume flows out of the Chesapeake Bay and turns south in response to the Coriolis force (to the right in the northern hemisphere). The result is a coastally trapped current that flows south. Plume position and strength are modified by wind forcing, tidal conditions, and river flow (Boicourt 1981, Boicourt *et al.* 1987). During the summer, winds are predominantly from the southwest at 8-10 m/s. This upwelling favorable wind spreads the plume offshore forming a lens of low salinity water 1-2 meters thick that can extend up to 50 Km from Cape Henry, VA (Norcross and Harrison 1967, Johnson 1987, Boicourt *et al.* 1987).

Coastal upwelling between the Chesapeake Bay Plume and the coast is also generated in response to southwesterly winds during summer. Upwelling is indicated by lower water temperatures and higher salinities in the near coastal areas (Paraso and Valle-Levinson 1996). Upwelling is not characterized by strong domed isotherms and isohalines off the Virginia coast, rather, the shallow shelf and low density surface plume create a strongly stratified two-layered system. Cold Pool Water (CPW) in bottom waters offshore can be transported to the inner shelf in response to both seasonal and meteorological driven upwelling (Hicks and Miller 1980). This further enhances seasonal water column

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stratification. The presence of this water mass on the inner-shelf is evidence for cross-shelf transport in response to upwelling.

Higher salinity water (>34) can also occur on the shelf. Instabilities in the Gulf Stream result in discharges of surface water that move onto the Virginia Shelf (Churchill *et al* 1993). Additionally, shelf-slope exchange can occur above the pycnocline in partial response to southwesterly winds. Flagg *et al.* (1994) found that intrusions of high salinity slope water (>35) at the shelf-slope front were in part associated with southwesterly winds. These intrusions may be important in transporting expatriate taxa from the slope sea into shelf waters (Hare and Cowen 1991, Cowen *et al* 1993) where local forcing can then modify their spatial distribution.

Methods and Materials

The Inner Shelf waters off the Chesapeake Bay mouth were sampled in a 42 station grid over 72 hours during a period of strong upwelling from August 26-30, 1988 (Fig 36). Stations were placed at 15 km intervals along 6 transects perpendicular to the coast and were sampled in sequence from the northwest to southeast corner of the grid. A last transect was added inshore parallel to the coast from False Cape to Cape Charles, VA.

At each station, salinity, temperature, dissolved oxygen and depth were recorded with a Seabird Electronics, Inc. CTD. Water samples were obtained at 5m depth intervals at alternating stations for Chlorophyll-a. Samples were collected by filtering 100 ml of sea water through 1.0 µm GF/F filters, and were frozen for later analysis using the methods of Parsons *et al.* (1984).

Wind speed and direction were obtained from the Chesapeake Light Tower (NOAA C-MAN station, 36° 54' N, 75° 42' W, NODC). These data were used to

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determine the potential for wind induced upwelling based upon wind direction and wind speed.

A standard MARMAP type bongo net (61 cm, 333µ and 505µ mesh) was used to obtain both double oblique and sub-surface (1m) samples (Sibunka and Silverman 1984) General Oceanics (model 2030) flowmeters were attached to each net in order to calculate the volume of water filtered. All ichthyoplankton were removed from the oblique and 1m (505µ) samples, enumerated and identified to the lowest taxonomic level. Abundance of larvae from 1-meter tows are reported as number/100 m^3, while abundance from oblique tows are reported as number/ 10m^2 of the sea surface

Data Analysis

Principal Component Analysis (PCA) was performed on ln-transformed, ln(x+1), abundances to derive and ordinate assemblages, *sensu* Sabates (1990) and Richards *et al* (1993). Data were normalized by subtracting the mean of the 42 samples for each taxa from each datum. PCA (NCSS Statistical System, Kaysville, UT) was applied to a Pearsons correlation matrix (species X sample) of all taxa having a mean abundance greater than 1.0/100 m^3 (sub-surface samples) or greater than 1.0 /10m^2 of the sea surface (oblique tows). A factor loading greater than 0.5 was used to define assemblage members. Members with the highest factor loadings were used as indicator taxa for the assemblages. Factor scores and indicator taxa were then correlated with environmental parameters using Spearman Rank Correlation. Unknown and unidentified taxa were excluded from the analyses.

Species assemblages were also described using hierarchical clustering techniques (NCSS). Unweighted Paired Group Averaging (UPGMA) was selected because it is

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flexible and robust (Gauch 1982). Dissimilarity was based upon Pearsons Product Moment correlations of the species retained for the PCA and was calculated using the absolute value of 1-r. The resulting dendrograms were used to delineate species assemblages, and were compared with the species ordination from the PCA. These two techniques were used to complement one another since PCA ordinates taxa in relation to unknown environmental gradients while CA classifies taxa relative to one another (Gauch 1982)

Atlantic croaker, *Micropogonias undulatus* and anchovy, *Anchoa* spp were measured to the nearest 0.1 mm (total length (TL) for pre-flexion larvae, standard length (SL) for post-flexion larvae) using the OPTIMAS imaging system (BioScan Inc., Edmonds, WA). No correction for shrinkage was applied. These measurements were used to examine whether larval size was associated with cross-shelf distance, by comparing length frequency distribution in surface waters at the most inshore and most offshore stations. The Kolmogorov-Smirnov test was used to test whether length frequency distributions were different between inshore and offshore in surface waters for each taxa

Results

Meteorological Forcing and Seasonal Upwelling

The summer of 1988 was dominated by an atmospheric high pressure system centered over Bermuda that resulted in upwelling-favorable conditions along the coast for most of the summer. These southwesterly winds averaged 8 m/s from early June through mid-August, after which winds became more variable (see Flagg *et al.* 1994)

The week prior to sampling, southwesterly winds changed to northeasterly and the mean velocity increased to nearly 10 m/s (Fig. 36). This northeasterly wind event lasted

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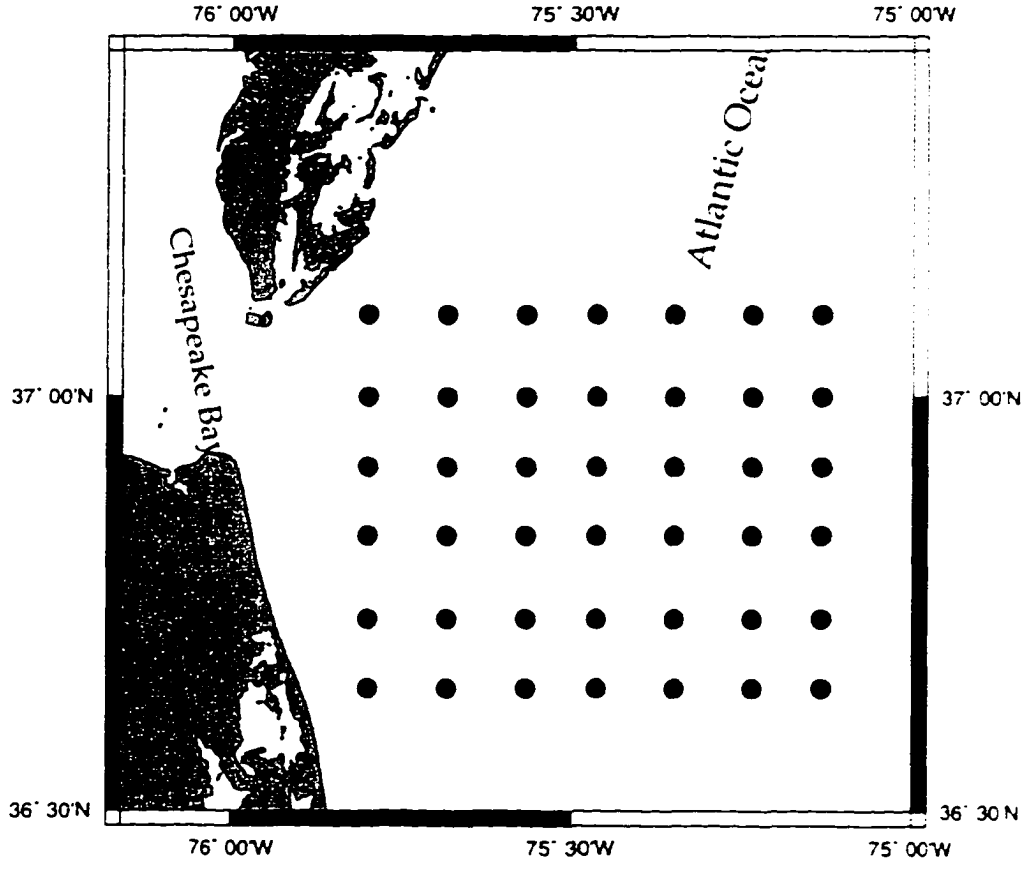

Figure 35. Map of sampling area over the Continental Shelf during the cruise from August 26-30, 1988

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approximately 2 days (Aug. 22-23) and forced the plume against the coast. Therefore, the sample allocation did not encompass as much of the plume area as planned. During the sampling period the winds reverted to southwesterly at approximately 5-7 m/s. These meteorological events created complex hydrographic conditions on the shelf.

Salinity and Temperature

Multiple water masses were present in the sampling area during the cruise and were identified by their temperature and salinity (T-S) relationships. Chesapeake Bay plume water was identified by low salinity (<32) and relatively high temperature (22 °C), while mid-Atlantic shelf water had a similar temperature range, but was more saline (>32-<34). Slope water was also present and was identified by high salinity (>35) and high temperature (>17 ^{0}C). In addition to these three water masses, a fourth water mass exhibited a characteristic T-S signal that classified it as Mid-Atlantic Cold Pool water (33 psu, <11^{0}C, CPW). The water column was highly stratified in response to wind induced upwelling (Fig. 38), and the presence of the CPW water near the coast below the pycnocline is the result. On all transects, a strong thermocline was visible that varied from 5m nearshore to 15 m at the offshore stations.

The coldest water (<11^{0}C) was present at depth along the middle of transects 1 (Fig. 38b) through 3 (Fig. 38d), while along transect 5 (Fig. 38f) the coolest waters occurred inshore along the coast and offshore. A strong halocline concurrent with the thermocline was not evident on all transects, although salinity increased in the offshore direction and with depth (Fig. 38 a, c, e). Offshore surface transport, in response to upwelling, was visible as a plume of low salinity water (<32.4) found at the offshore stations in transects 3-5 (Fig. 38c and 38e). This is most evident along the fifth transect

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(Fig. 38e) where the halocline is continuous along the transect.

In addition to the upwelling and the offshore transport of plume waters, there was evidence of warm, high salinity slopewater within the sampling area. Slopewater (>35 psu, >18 ^{0}C) was visible at a depth of 10-15m at the end of transects 1 and 2. This slopewater overlies cold, dense CPW and is also visible as a depressed thermocline (Fig. 38a). Higher salinity water (>34) extended closer to shore in each transect, so that on transect 5 high salinity water was enveloped on either side by cold and less saline water.

Contour plots of surface temperature varied less than 4.5 degrees across the sampling area and did not a show strong pattern (Fig. 39a). Temperatures were lower (<22 ^{0}C) in the northwestern part of the grid close to the bay-mouth, and generally increased to the south and offshore. This is, in part, a consequence of cold upwelling water mixing with the plume near the coast. Surface salinity (1m) patterns were consistent with wind induced transport of low salinity coastal or plume water to the shelf (Fig. 39b). Salinity ranged from <30 psu nearshore to >33 psu in some areas of the grid. Near the coast a frontal region with rapid salinity change separated water < 31 psu from higher salinity coastal water that was transported to the shelf.

At 10m cross-shelf distribution of temperature and salinity was less complex and low salinity water was not visible offshore (Fig. 39 c-d). Low temperature water (< 11 ^{0}C) was observed in the center of the grid and was surrounded on all sides by warmer water. The temperature gradient exceeded 8^{0}C from the center of the grid to the northeast edge. Based on salinity, no plume water was evident (<30 psu) at 10m, however, shelf water (33 psu) and cold pool water were present inshore. The Cold Pool water must have been

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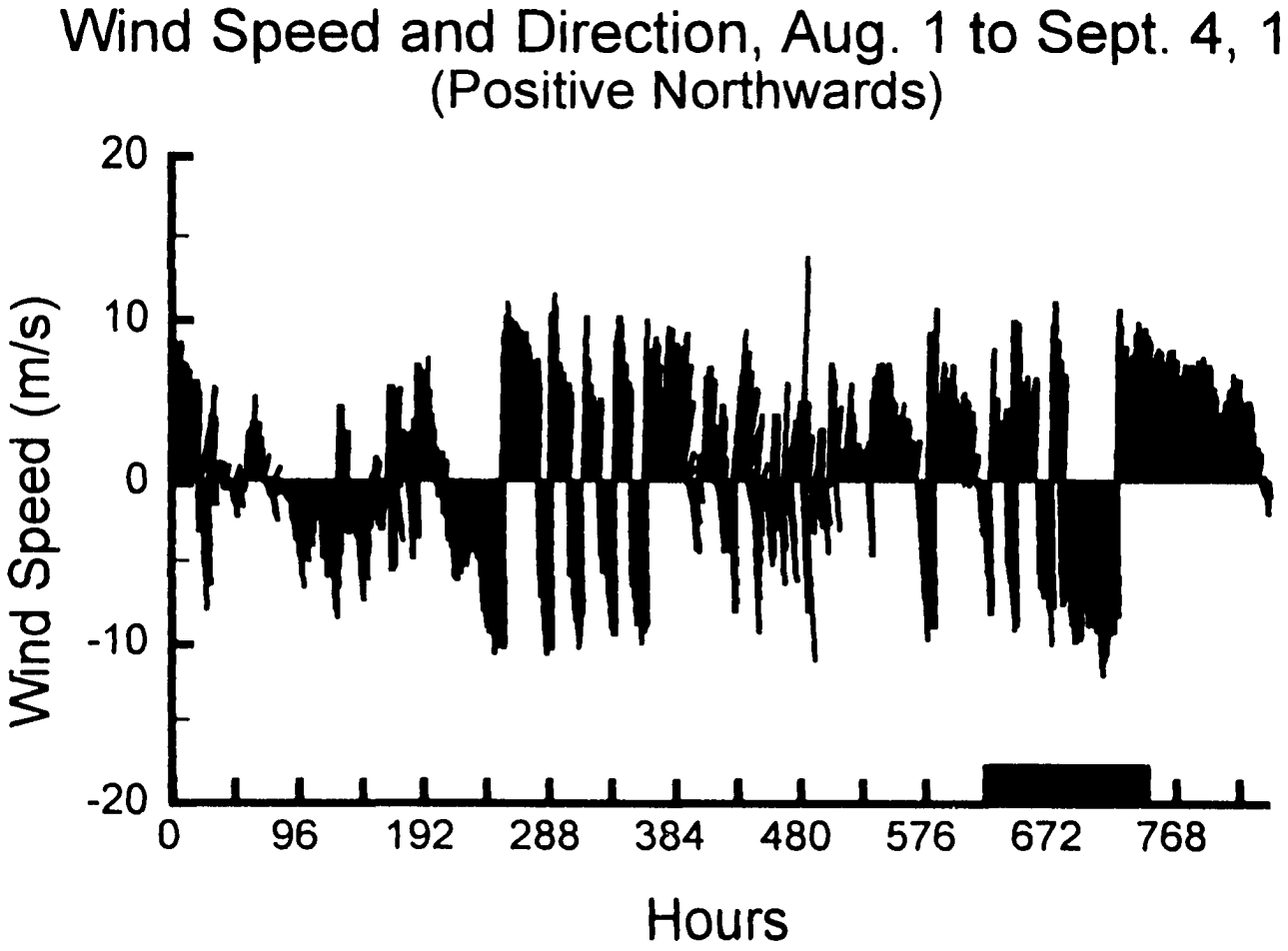

Figure 36 Wind Speed (m/s) and direction (positive northwards) from August 1 to September 4, 1988 The black bar shows the sampling period, from August 26-30, 1988

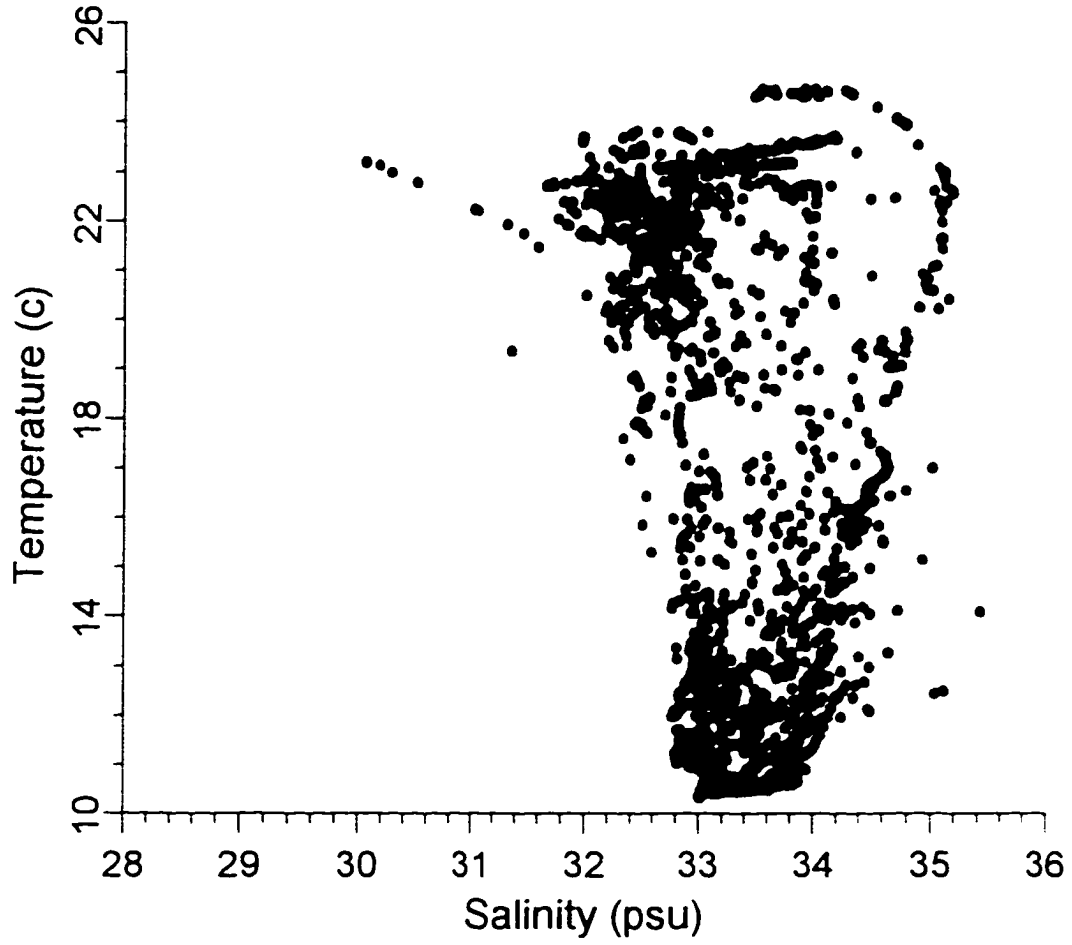

Figure 37 Temperatures and salinity relationship for stations occupied during the cruise period (n=39)

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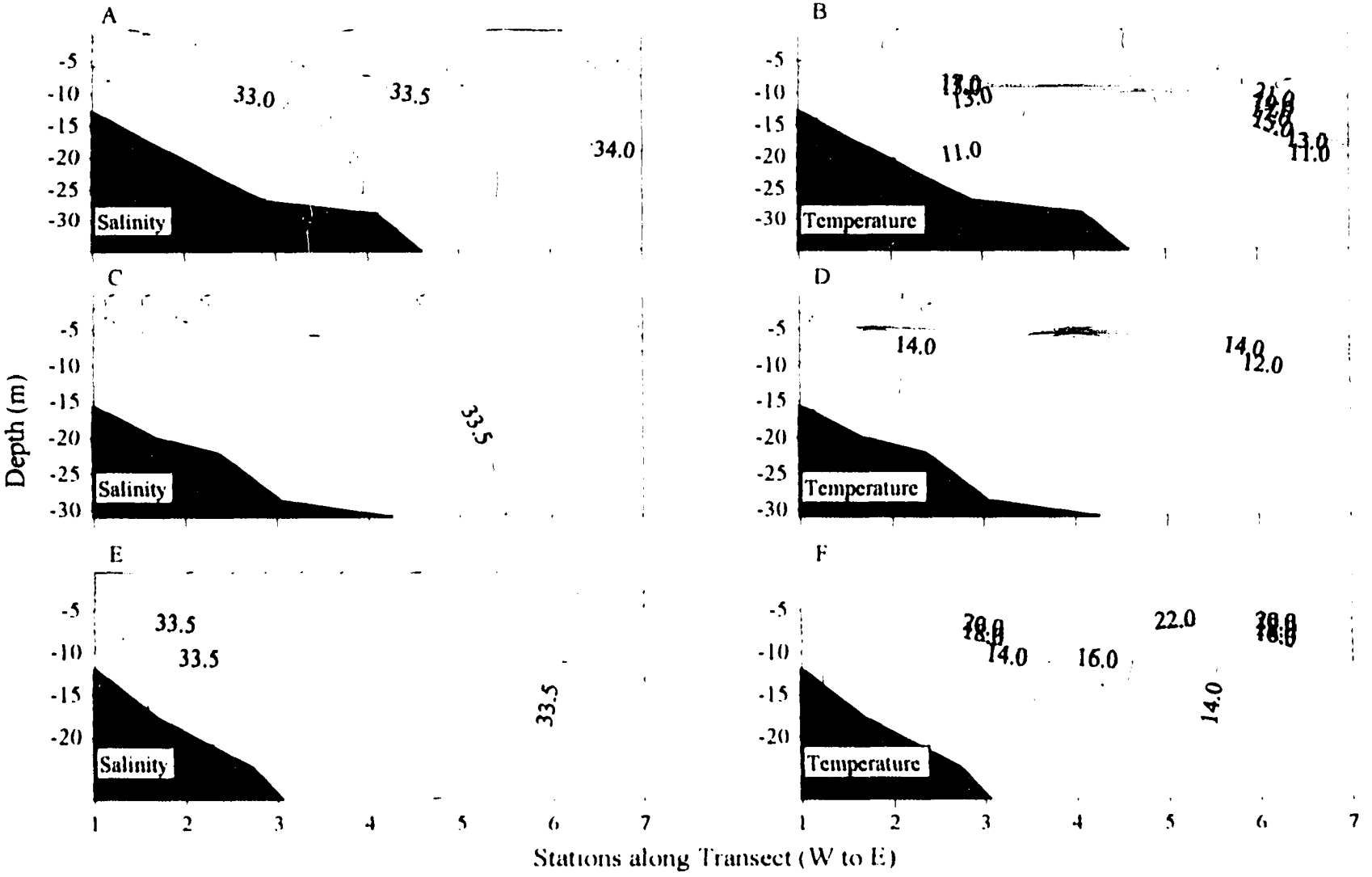

Figure 38 Isotherms and isohalines for transects 1, 3, 5 across the inner shelf, August 1988 (A) Salinity transect 1, (B) Temperature (°C) transect 1, (C) Salinity Transect 3, (D) Temperature (°C) Transect 3, (E) Salinity Transect 5, (F) Temperature (°C) transect 5

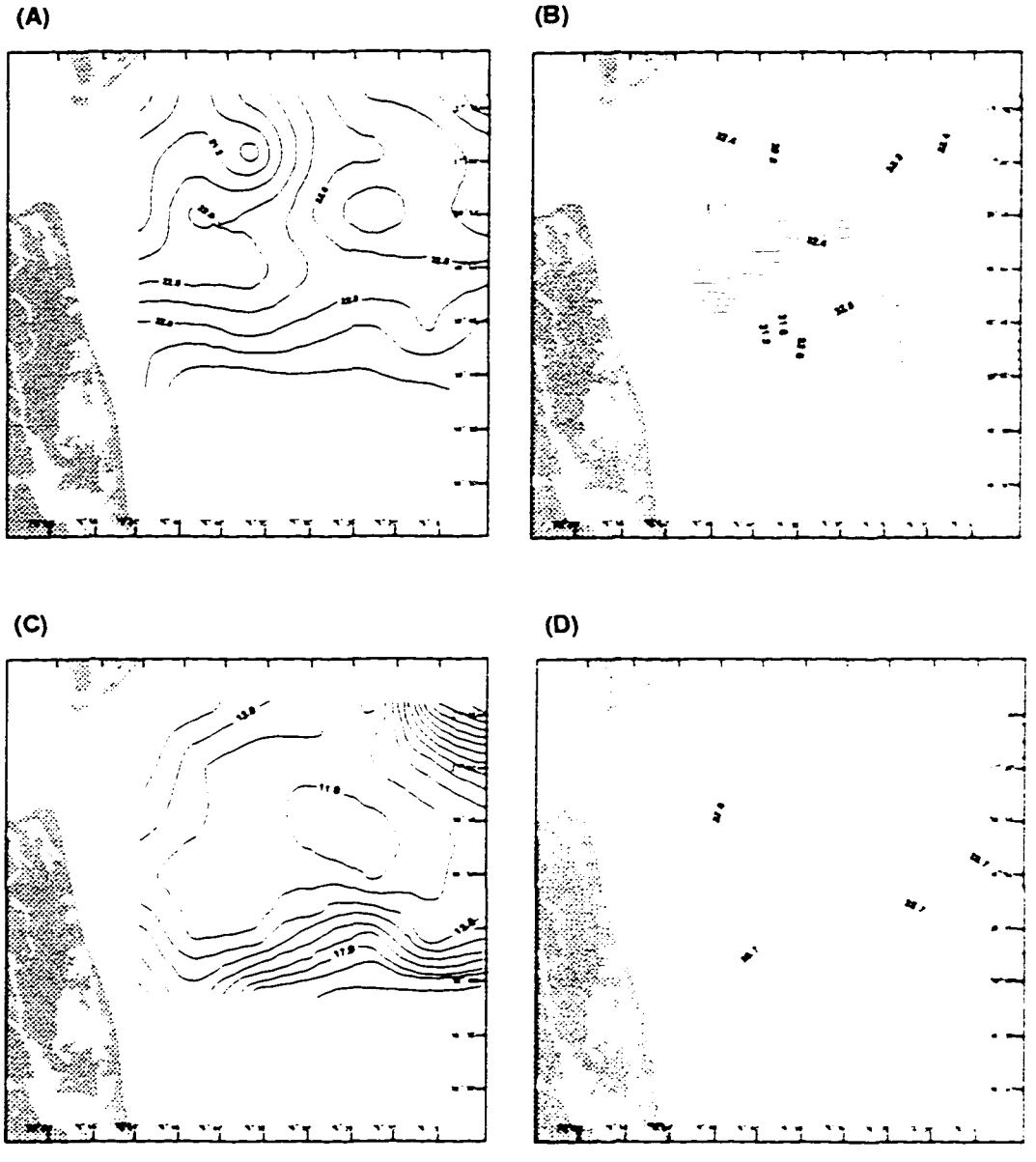

Figure 39 Isopleths of salinity (psu) and temperature (^{o}C) during the sampling period, August 26-30, 1988 (A) temperature at 1 meter, (B) salinity at 1 meter, (C) temperature at 10 meters, (D) salinity at 10 meters

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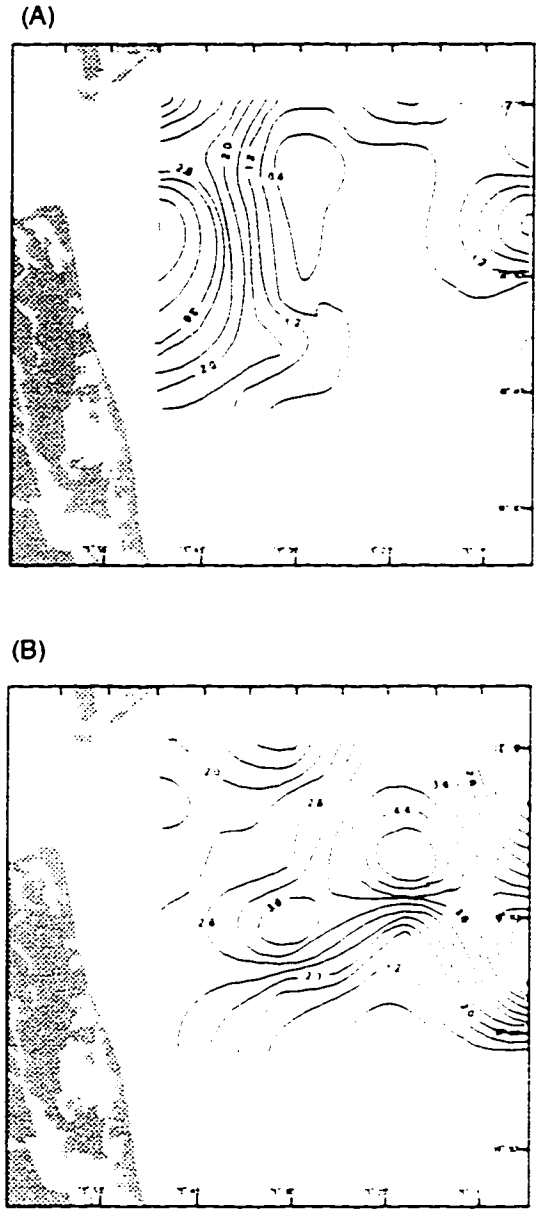

Figure 40. Isopleths of chlorophyll-s concentrations (μg/L) across the shelf, August 26-30, 1988. (A) surface waters; (B) 10 meters

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Table 14. Ranked mean abundance (#/10m^2 sea surface), standard deviation (Std Dev.), and maximum number of ichthyoplankton collected Aug. 26-30, 1988 in the oblique tows. Taxa are ranked in order of decreasing mean abundance for all stations. * = mean less than 0.2/10m^2 sea surface.

Variables	Mean	Std. Deviation	Maximum
Etropus microstomus	139.3926	178.001	748.6108
Symphurus spp.	129.4002	114.6467	479.3736
Prionotus spp.	67.13196	99.10873	426.2821
Anchoa sp. 1	48.49569	82.06676	394.6613
Micropogonias undulatus	30.67782	98.03152	589.2888
Ophidion spp.	27.36295	25.39763	86.2196
Centropristis striata	16.25184	21.88841	82.36994
Citharichthys arctifrons	9.037951	24.93128	152.5641
Astroscopus guttatus	8.322051	11.20878	44.87179
Scombridae	4.006003	12.51144	72.9853
Carangidae	3.526192	8.661182	49.25283
Unknown 2	3.125749	5.230327	19.80028
Cynoscion nebulosus	2.772128	5.414843	24.32843
Unknown 1	2.726378	5.610593	23.46753
Bothus spp.	2.369673	4.390106	15.90203
Xyrichtys novacula	1.928586	4.872844	28.01724
Synodus spp.	1.717047	3.816202	17.34104
Blenniidae	1.310277	3.688755	16.12904
Menticirrhus spp.	1.108079	2.809892	14.00862
Gobiidae	0.6616957	1.592617	6.628787
Leiostomus xanthurus	0.5239527	2.477934	15.55352
Bairdiella chrysura	0.3816569	1.727637	8.109478
Anguilla leptocephalus	0.3639937	1.413166	6.608359
Larimus fasciatus	0.2838963	1.099767	5.866883
Rachycentrum canadum	0.2770521	1.266861	6.632277
Serranidae	*	1.023383	6.632277
Anchoa sp. 2	*	1.022844	6.628787
Tetraodontidae	*	1.022844	6.628787
Syacium papillosum	*	0.6952758	3.749332
Peprilus triacanthus	*	0.9643959	6.25
Glyptocephalus cynoglossus	*	0.9643959	6.25
Syngnathus fuscus	*	0.5139638	3.330866

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Table 15. Ranked mean abundance (#/100m^3), standard deviation (Std. Dev.) and maximum mean for ichthyoplankton collected Aug. 26-30, 1988 in surface (1 m) tows. Taxa are ranked in order of decreasing mean abundance for all stations. * = mean less than 0.2 #/100m^3

Variables	Mean	Std. Deviation	Maximum
Symphurus spp.	26.47025	34.36232	139.4759
Prionotus spp.	11.40851	13.60414	52.57115
Etropus microstomus	7.752758	15.10413	76.74597
Anchoa sp. 1	6.504204	11.85527	60.68732
Astroscopus guttatus	4.122497	4.111479	13.52494
Micropogonias undulatus	3.507523	12.88976	79.74032
Scombridae	2.011739	6.591722	40.92866
Ophidion spp.	1.671529	3.006059	15.21555
Carangidae	1.336982	2.270549	9.942829
Centropristis striata	1.237101	4.296481	27.19197
Blenniidae	1.130332	3.899735	22.34498
Menticirrhus spp.	1.098348	3.231439	20.46433
Cynoscion nebulosus	0.7539031	1.6786	7.491147
Peprilus triacanthus	0.6537024	1.596582	8.699975
Bothus spp.	0.4679242	0.9032553	4.187605
Pomatomus saltatrix	0.3504788	0.9032971	3.745599
Citharichthys arctifrons	0.2773632	0.5127518	2.093802
Syngnathus fuscus	*	0.4824713	2.948693
Xyrichtys novacula	*	0.3847435	1.705466
Synodus spp.	*	0.3339597	1.589825
Unknown 1	*	0.3315022	1.86428
Gobiidae	*	0.2626294	1.241388
Anguilla leptocephalus	*	0.1726739	0.8858965
Tetraodontidae	*	0.1166994	0.557072

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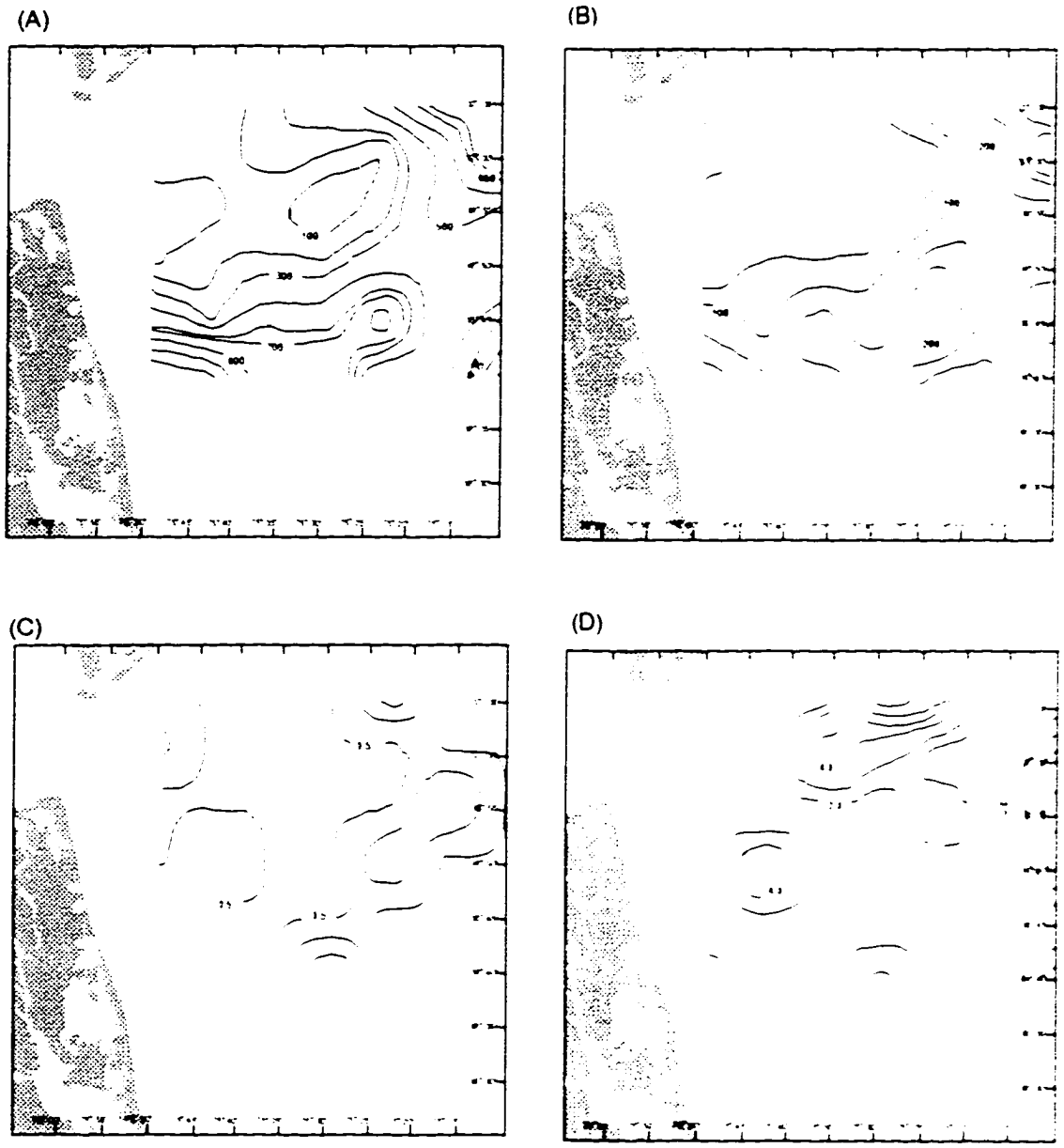

Figure 41 Isopleths of ichthyoplankton (#/10 m^2 sea surface), Aug 26-30, 1988 (A) total ichthyoplankton, (B) indicator taxa for Factor 1 (*Symphurus* spp), C) indicator species for Factor 2 (*Menticirrhus* spp), (D) indicator species for Factor 3 (*Bothus* spp)

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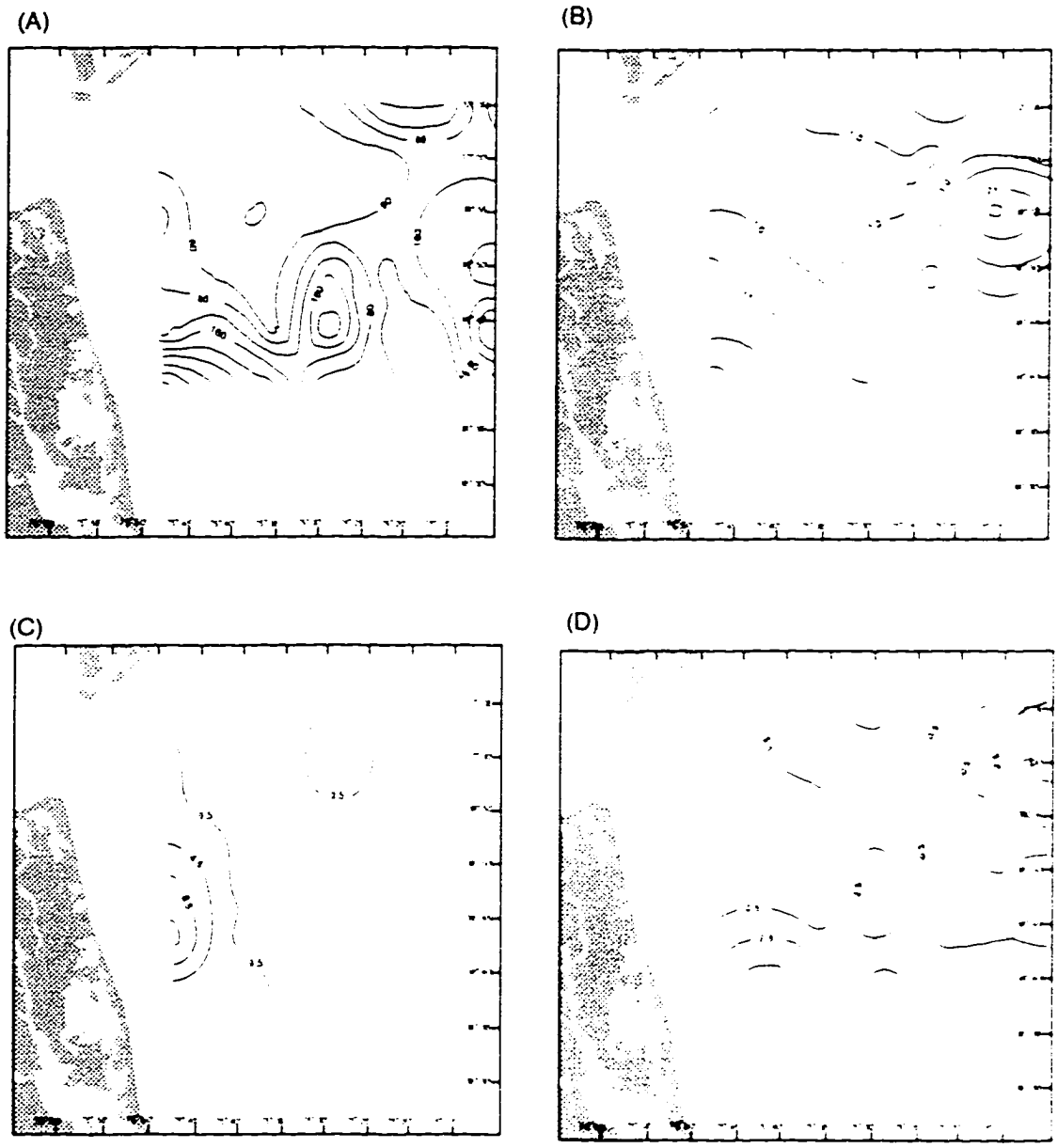

Figure 42. Isopleths of ichthyoplankton (#/100 m^3) on the surface (1-meter) tows, Aug 26-30, 1988. (A) total ichthyoplankton, (B) indicator species for Factor 1 (*Anchoa* spp.), (C) indicator species for Factor 2 (Blenniidae), (D) indicator species for Factor 3 (Carangidae).

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transported to the coast, presumably as a result of upwelling

Chlorophyll-a

Cross-shelf chl-a distributions showed peaks associated with the low salinity water near the shore and offshore at the surface (Fig. 40a). At 10m (Fig. 40b), chl-a concentrations reached maxima (>4 μg/L)and corresponded to the cold water near the pycnocline in the center of the sampling grid (Fig. 39c). These distributions indicate that chl-a was transported offshore in the plume waters at the surface, while production or concentration of chl-a occurred at depth.

Distribution of Ichthyoplankton - Oblique tows

A diverse group of larvae were collected in oblique tows. Only *Symphurus* spp. and *Etropus microstomus* were nearly ubiquitous occurring at 41 and 40 of the 42 stations (Table 14). The ten most common taxa represented >90% of all larvae collected. There was no inshore to offshore gradient in the distribution of bay-spawned or near coastal spawned taxa. Instead, the larval distributions followed the salinity distribution at the surface. Highest larval abundances occurred within the southernmost coastal areas (>1500/10m^2), while lower concentrations (>100/10m^2) occurred around the outer perimeter of the sampling grid. The lowest larval abundances (< 100/10m^2) occurred in the center of the sampling grid (Fig. 41a). This pattern is consistent with offshore transport of larvae within a plume of low salinity water.

Of the 30 ichthyoplankton taxa collected in the oblique tows, 17 were used in the PCA, and the first 3 principal components explained 29.09%, 14.23%, 11.58% of the variance, respectively. Based upon the highest factor loading for each principal component, the three indicator taxa were *Symphurus* spp. (Factor 1), *Menticirrhus* spp.

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(Factor 2), and *Bothus* spp. (Factor 3). Factor 1 loadings comprised the 10 most abundant taxa collected (Table 16), including *Symphurus* spp. (Fig. 41b), *Synodus* spp. *Astroscopus guttatus*, *Prionotus* spp., *Ophidion* spp., *Anchoa* sp. 1, *Centropristis striata*, *Etropus microstomus*, Scombridae, Carangidae 1. and *Micropogonias undulatus*. Factor 2 was composed of six taxa, *Menticirrhus* spp. (Fig. 41c), *C. nebulosus*, Blenniidae, *Anchoa* sp. 1, *Ophidion* spp., and *C. striata*. The loadings suggested that this factor was contrasting plume taxa from shelf taxa, as high loadings for plume taxa were negative and high loadings were positive for the shelf taxa. Factor 3 was composed of three taxa of which two were expatriates, *Bothus* spp. (Fig. 41d) and *Xyrichthys novacula*.

Temperature, salinity and chlorophyll-a at the surface and at 10 meters was correlated with factor scores from the PCA. Factor 1 was negatively correlated with temperature and salinity at 10 meters and with temperature at 1m (Table 18). This may reflect the influence of both the sub-surface and surface waters influencing the distribution of larvae. Factor 2 and Factor 3 were both significantly correlated with salinity at 1m, $r=0.5347$ ($p<0.0005$), and $r=0.4580$ ($p<0.0034$), respectively. These correlations support the ordination of taxa with environmental parameters, principally shelf-vs-plume taxa, and the presence of an expatriate assemblage. Correlations between the indicator taxa from the PCA, found significant correlations between *Symphurus* spp. (the indicator taxa for Factor 1) and temperature at 1m ($r=0.6704$, $p<0.0001$), while neither *Menticirrhus* spp. (Factor 2) or *Bothus* spp. (Factor 3) were significantly correlated with any measured variable.

Cluster analysis failed to reveal any distinct clusters of larvae that would corroborate the results of the ordination (Fig. 43a). The cluster analysis grouped known plume, (*Anchoa* sp. 1) and shelf taxa (*Etropus microstomus*) together, but also placed

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Table 16. Factor loadings between species and the first three principal components for oblique tows. Factor loadings that are in bold type represent indicator species for that factor. High (>0.50) loadings represent members of the species assemblages.

Variables	Factor 1	Factor 2	Factor 3
***Symphurus* spp.**	**-0.76044**	-0.14933	-0.05484
Synodus spp.	-0.69177	0.06155	-0.21156
Carangidae	-0.67418	0.07157	0.35283
Ophidion spp.	-0.66152	0.58399	0.10627
Centropristis striata	-0.6574	0.59235	-0.17092
Astroscopus guttatus	-0.64939	0.34623	0.2504
Etropus microstomus	-0.64111	0.06579	-0.39545
Prionotus spp.	-0.62467	-0.05506	0.2691
Anchoa sp. 1	-0.6145	-0.56982	-0.08798
Scombridae	-0.53853	-0.1551	-0.29833
Micropogonias undulatus	-0.52481	-0.28856	0.5024
Citharichthys arctifrons	-0.44065	0.09812	-0.11266
Blenniidae	-0.3041	-0.53224	0.3594
Cynoscion nebulosus	-0.19281	-0.58393	0.17264
***Menticirrhus* spp.**	-0.18644	**-0.67346**	-0.18794
***Bothus* spp.**	-0.18267	-0.21406	**-0.76457**
Xyrichthys novacula	-0.08384	-0.05532	-0.62146

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Table 17. Same as table 17, except for 1 meter tows.

Variables	Factor 1	Factor 2	Factor 3
***Anchoa* sp. 1**	**-0.84186**	0.30640	0.01110
Scombridae	-0.81056	0.21232	-0.26624
Symphurus spp.	-0.80853	-0.22185	0.22589
Etropus microstomus	-0.75066	-0.31143	-0.22513
Menticirrhus spp.	-0.72345	0.48822	0.11919
Ophidion spp.	-0.66565	-0.48707	0.26399
Micropogonias undulatus	-0.64907	0.64391	0.05653
Prionotus spp.	-0.62859	-0.29650	0.32409
Centropristis striata	-0.58029	-0.38332	-0.30065
Astroscopus guttatus	-0.57666	-0.47910	0.29852
Carangidae	-0.45034	-0.20541	**-0.73429**
Blenniidae	-0.42802	**0.73308**	0.05478

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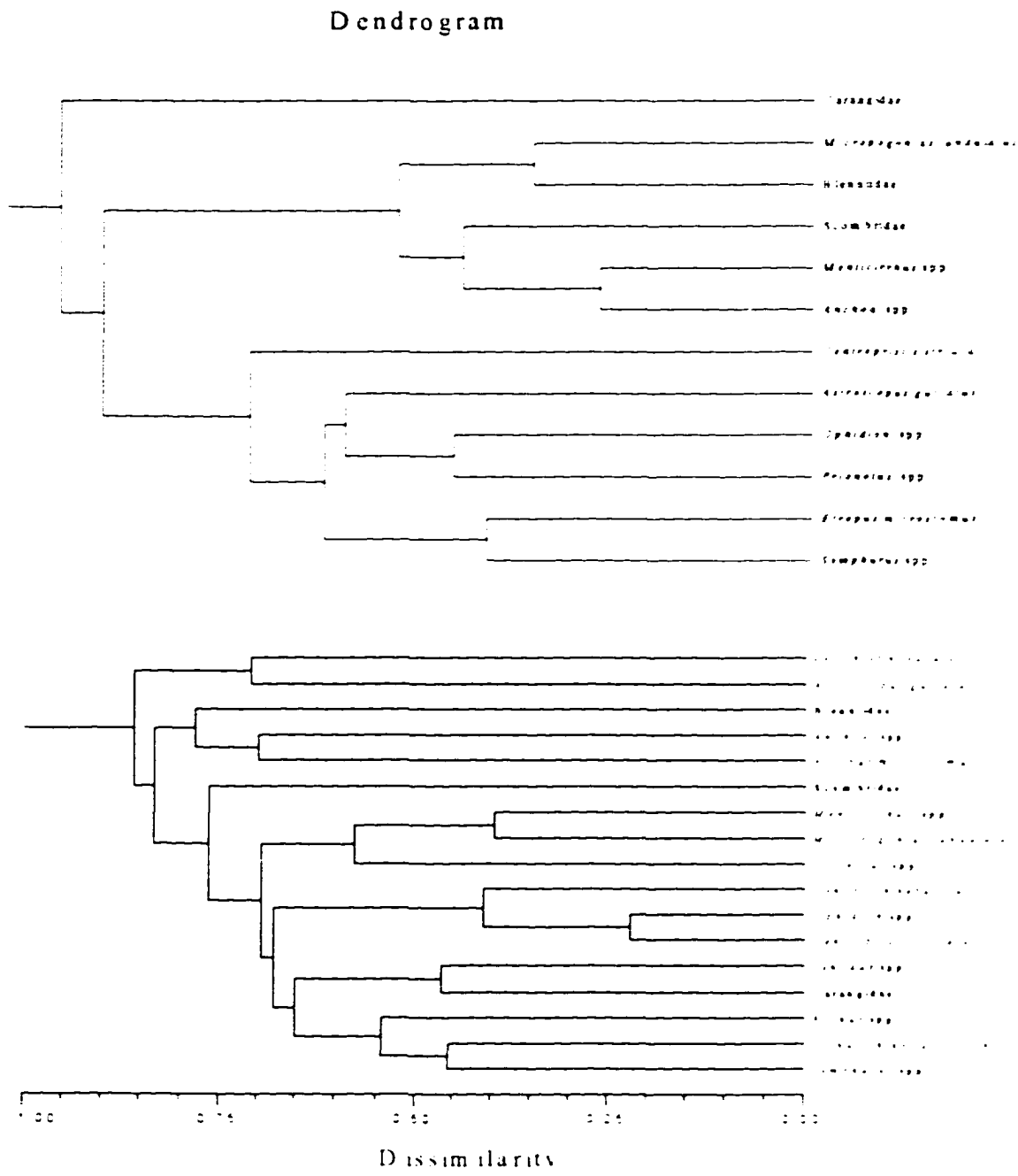

Figure 43 Dendrogram of species clusters from UPGMA clustering using absolute value of (1-r) of the correlations as a dissimilarity measure (A) Dendrogram for 1 meter tows. (B) Dendrogram for oblique tows

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known expatriate taxa (*Xyrichtys novacula* and *Bothus* spp) in the same clusters as shelf taxa like *Astroscopus guttatus* and *Symphurus* spp. These findings suggest that while PCA was able to ordinate larvae along the principal environmental gradient (salinity and temperature) CA was unable to classify known assemblages, probably because the oblique tows sampled above and below the pycnocline, combining shelf and plume taxa

Distributions of Ichthyoplankton: sub-surface tows (1m)

The spatial pattern of ichthyoplankton in sub-surface waters, although patchy, was similar to the pattern described for the oblique tows. Larval density at the southernmost stations near the plume exceeded 300/100m^3, while larval densities at northern, offshore sampling stations were >100/100m^3 offshore (Fig. 42a) Larval densities within the central portion of the grid were <10/100m^3 Twenty-three taxa were identified in the sub-surface (1m) samples, and *Symphurus* spp and *Prionotus* spp. were the two most abundant taxa collected (Table 15) with mean abundances of 26 5 and 11 4 100 m^3, respectively

PCA of sub-surface samples ordinated taxa better than in the oblique tows Twelve taxa with mean densities greater than 1 0/100m^3 were kept for this PCA, and the first three principal components explained 72 72 % of the variance of all components The first three factors explained 45 18 %, 18 49 % and 9 05% , respectively Indicator taxa, based upon the highest factor loadings of each principal component were *Anchoa* sp. 1 (Factor 1), Blenniidae (Factor 2), and Carangidae (Factor 3) (Table 17)

As in the oblique PCA, Factor 1 described a large percentage of the variance, but included all taxa with high densities and broad distribution across the shelf (Fig 42b) Factor 1 was composed of *Anchoa* sp 1, Scombridae, *Symphurus* spp., *Menticirrhus* spp *Etropus microstomus*, *Ophidion* spp., *Prionotus* spp., and *Micropogonias undulatus*

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Factor 2 was represented by two taxa, Blenniidae and *M. undulatus*, while Factor 3 was represented by only a single taxa, Carangidae (Fig. 42c-d). Missing from this ordination were *X. novacula* and *Bothus* spp. taxa that influenced the ordination of the oblique tows.

Correlations between the factor scores and environmental parameters at 1m showed significant associations (Table 18). Factor 1 was negatively correlated with temperature ($r=-0.5227$, $p<0.0006$) and chlorophyll-a ($r=-0.5318$, $p<0.013$), while positively correlated with salinity ($r=0.4262$, $p<0.006$), indicating that larvae associated with factor 1 were ordinated with the plume. Neither Factor 2 or Factor 3 were significantly correlated with any physical or environmental parameter.

Correlations between the indicator taxa and the 1m environmental variables were also performed. *Anchoa* sp. 1 (the indicator taxa for Factor 1), was positively correlated with surface temperature ($r=0.5038$, $p<0.001$), and was not significantly correlated with either chlorophyll-a ($r=0.4764$, $p<0.0290$) or surface salinity ($r=-0.4182$, $p<0.008$). Neither Blennidae (the indicator taxa for Factor 2) or Carangidae 1 (the indicator taxa for Factor 3) were significantly correlated with any environmental parameters.

There was a strong grouping of taxa in the surface tows when cluster analysis was applied (Fig. 43b). Two distinct clusters emerged, and one taxa did not attach to any clusters. The first assemblage comprised *Symphurus* spp., *Etropus microstomus*, *Prionotus* spp., *Ophidion* spp., *Centropristis striata* and *Astroscopus guttatus*. The second cluster was composed of five taxa, *Anchoa* sp. 1, *Menticirrhus* spp., Scombridae, Blenniidae and *Micropogonius undulatus*. The one taxa that did not cluster with others was Carangidae, the indicator taxa for Factor 3 (Fig. 43a). The assemblages derived by

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Table 18. Spearman rank correlations of the PCA factor scores on environmental parameters. significance at alpha = 0.005

TOW TYPE	PARAMETER	n	FACTOR 1	FACTOR 2	FACTOR 3
OBLIQUE					
	TEMP 1M	39	-.5881 (.0001)	NS	NS
	SALINITY 1M	39	NS	0.4691 (.0020)	-0.5197 (.0006)
	TEMP 10M	38	-.5297 (.0006)	NS	NS
	SALINITY 10M	38	-.6173 (.0001)	NS	NS
	CHL-A 1M	20	NS	NS	NS
	CHL-A 10M	22	NS	NS	NS
1 METER					
	TEMP 1M	39	-.5227 (.0006)	NS	NS
	SALINITY 1M	39	.4262 (.0060)	NS	NS
	CHL-A 1M	20	-.3908 (.01398)	NS	NS

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CA differed from the PCA principally by separating the members of factor 1 in the PCA into two groups, one group reflecting most of the shelf taxa and a second combining mostly plume taxa with several typically shelf taxa (Scombridae and *M. undulatus*)

Length Frequency Analysis of Surface Samples

The classification of *Anchoa* spp with *M. undulatus* together in sub-surface samples was explored further to determine why the CA was clustering taxa historically associated with different assemblages (Olney 1996) The length frequency data for both *Anchoa* spp and *M. undulatus* showed trends of increasing size with distance offshore *Anchoa* sp. 1 showed a bi-modal distribution at both inshore and offshore locations (Fig 44 a-b). The size-range and length frequency distribution differed between locations, 2.25-21.5 mm inshore, and 4 5-17 5 mm offshore (α=0 05, p<0 0015) In contrast to *Anchoa* spp., *Micropogonias undulatus* larvae showed unimodal distributions inshore and offshore in the surface waters (Fig. 44 c-d), with lengths ranging from 1 5-5 5 mm inshore to 2-4 75 mm offshore The length frequency distributions were significantly different (α=0 05, p <0 005) These data suggest that these two larval taxa were transported to the shelf from the coast, presumably with the plume of low salinity water at the surface

Discussion

Southwesterly winds combined with seasonal stratification resulted in upwelling during much of the summer of 1988 This affected the spatial distribution of larvae on the shelf. The effect of coastal upwelling was evident on the inner shelf as a plume of low salinity water extending offshore in the surface and also as sub-pycnocline Cold Pool

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Water (~ 33, <11^{0}C) extending to the near shore area. Mid-Atlantic Cold Pool Water (CPW) is present on the inner shelf in increasing amounts as the summer progresses (Houghton and Marra 1983) and is transported from the mid-shelf to the shore quickly (<24 hours) during more forceful upwelling conditions (Hicks and Miller 1980). The observed pattern in both surface and bottom waters is consistent with the rapid transport of those water masses in response to meteorological forcing.

Both oblique and 1m samples were dominated by inner-shelf, near-coastal and plume taxa, but many offshore and expatriate taxa were also captured in the oblique tows. While the numbers and types of larvae collected were similar to the findings by Olney (1996), neither the PCA or the cluster analysis of oblique tows resolved the assemblages that Olney found. The derived assemblages were not tightly correlated to salinity or temperature and reflected the contamination of the sub-pycnocline water with plume water and its associated larvae in the oblique tows.

The second principal component of the oblique tows separated plume taxa from shelf taxa, while the third factor resolved an expatriate assemblage composed of *Bothus* spp. and *X. novacula*, (Cowen *et al.* 1993). This third assemblage was virtually absent from the study by Olney (1996), and suggests that upwelling conditions transported these larvae to the inner-shelf where they are not normally found.

The presence of expatriate taxa such as *Xyrichtys novacula*, *Bothus* spp. and other taxa such as *Glyptocephalus* spp. in the cold or high salinity waters of the sampling area support the hypothesis of extensive cross-shelf transport of either cold pool or offshore water in response to coastal upwelling.

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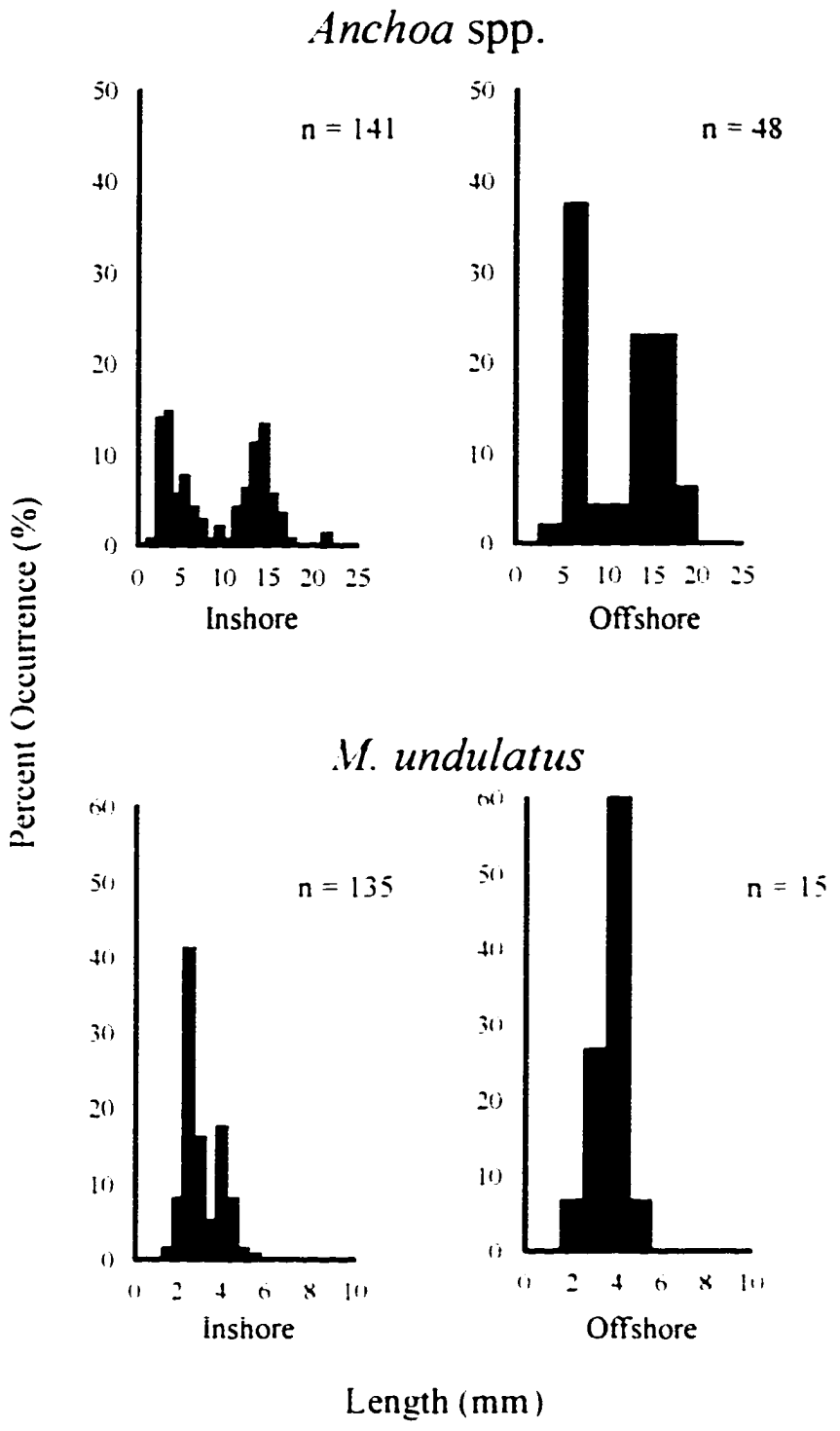

Figure 44 Length frequency histograms for (A) *Anchoa* spp at inshore locations, (B) *Anchoa* spp at offshore locations, (C) *Micropogonias undulatus* inshore, (D) *Micropogonias undulatus* offshore

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For *X. novacula* a mechanism for transport has been described (Hare and Cowen 1991). Warm Core Ring (WCR) impingement onto the shelf was correlated with the presence of this species in the MAB and George's Bank, suggesting that larvae were entrained within the Gulf Stream and transported north from the spawning area in the South Atlantic Bight. They found evidence that cross shelf transport of *Xyrichtys novacula* from continental slope waters to the shelf occurred along the pycnocline above the cold pool water in the MAB off of New York. Under appropriate conditions these intrusions can extend to the inner continental shelf where local forcing can be important in the distribution of expatriate and shelf-spawned estuarine-dependent taxa (Johnson 1987, Boicourt and Hacker 1976). Upwelling may be the principal mechanism responsible for the local distributions of expatriates once they are on the shelf.

The ordination of sub-surface (1m) samples along the first PC explained much more of the variability than for the oblique samples. (42.7% compared to 25.4%). This reflects the fact that larvae from above and below the pycnocline were not combined as they were in the oblique tows. Cluster analysis of the species matrices for 1 m samples produced assemblage groupings that differed from Olneys' (1996) study principally in classifying both *Anchoa* sp. 1 and *M. undulatus* larvae together. These two taxa shared similar cross-shelf distributions. The differences in length frequency between inshore and offshore indicated that the larvae were transported from the coast to the shelf.

The co-occurrence of small *M. undulatus* a shelf-spawned, estuarine-dependent taxa, with *Anchoa sp.* 1 in surface tows suggests that *M. undulatus* may be spawning in the vicinity of the Chesapeake Bay plume front, rather than on the mid-shelf (Norcross 1983, 1991, Olney 1996). One other study has found ripe-running and recently spawned

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female croaker within the bay suggesting that spawning may be occurring earlier in the season and closer to shore (Barbieri *et al* 1993) Our hypothesis, that *M. undulatus* is spawned in the vicinity of the plume front at least early in the spawning season, in part explains the observed spatial pattern. Nearshore spawning would also explain its affinity for plume taxa like *Anchoa sp.* 1 and Blennidae, rather than shelf taxa like *Etropus microstomus*. If frontal or nearshore spawning is occurring, then the frequency and intensity of upwelling events that transport small larvae to the shelf may affect intra-seasonal survival.

During this study advection dominated over mixing processes and clearly affected the spatial pattern and heterogeneity of larvae on the shelf The short time scale over which the distributions arose raises several questions Are plume or near coastal larvae that are transported offshore lost to the shelf as hypothesized by Norcross (1991), or could they return as late stage larvae or juveniles if reversals in the wind field would transport them back towards the Bay Mouth? An example of a species with this reproductive strategy is the blue crab larvae, *Callinectes sapidus*. Blue crab larvae are exported from the Chesapeake Bay Mouth to offshore areas to develop before being transported back into the Chesapeake Bay (Johnson 1985, McConaugha 1988), and other Mid-Atlantic Bight estuaries (Epifanio 1988) during wind driven events The relatively well defined patches of ichthyoplankton, principally *Anchoa sp.* 1, concurrent with high chlorophyll-a concentrations and with blue crab larvae (McConaugha *et al* unpublished data) increases the possibility that some bay-plume species (i e *Anchoa sp.* 1) and near coastal species (such as *M. undulatus*) may be able to survive on the shelf until wind reversals force water back towards the baymouth

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Clearly, the distributions of ichthyoplankton across the shelf during this period were not related solely to temperature and salinity, but appear to be associated with the broad scale, wind mediated events occurring on small (days) time scales Future studies that wish to examine the spawning, distribution and transport of individual taxa must take into account the stochastic processes inherent in this shallow shelf system Finally, comparisons between upwelling, variable and downwelling conditions should be conducted to determine whether any of these processes may be controlling the survival, growth or recruitment of estuarine dependent or coastal taxa in Virginia Shelf waters

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CHAPTER 6

Discussion and Future Research

Spatial Patterns

The importance of riverine plumes and linear oceanographic features such as fronts on the spatial distribution, transport and survival of larval fish has been reviewed by Grimes and Kingsford (1996) and Kingsford (1990) They concluded that the spatial and temporal scale of these features was important and affected transport and survival of larvae. The present studies varied widely in scale, and yet reflected the importance of physics in determining the spatial pattern of larvae from the smallest scales (~ 1 km) to the largest scales sampled (15 km) Additionally, changes in vertical distribution were found that may enhance the separation of plume and shelf assemblages, reinforcing the physical separation provided by this estuarine-plume front

At the smallest scales sampled (~ 1 km) the distribution of ichthyoplankton within the Chesapeake Bay mouth was associated with the individual water masses in which larvae developed. In general, larvae from inshore and offshore were separated by density differences defined by the pycnocline or the front There was however, evidence that larval assemblages were mixed together over the shoals (chap 4) Mixed water over shoals is retained in place through bottom friction and inertia and consequently has a longer residence time within the baymouth than surrounding plume or shelf waters This increased residence time may enhance larval retention within the bay, but may also affect

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predation rates on larval fish or eggs as compared to stratified waters (Govoni and Olney 1991).

Cross-frontal transects onto the shelf during the summer of 1994 showed that the plume front was the principal mechanism separating estuarine larvae from shelf larvae. At larger spatial (>3 5 km) and temporal scales (bi-weekly), cross-frontal larval assemblages were shown to be temporally stable although dominant taxa within both plume and shelf assemblages varied seasonally. This contrasts with the conclusion drawn by Olney (1996) who proposed that larval assemblages were mixed together producing an assemblage composed of plume and shelf taxa. In the current study the seaward distribution of plume taxa, especially *Anchoa* spp., was determined by the seaward extent of the outflow plume or plume front. At least one estuarine spawned taxa, *Symphurus* spp., showed evidence of an ontogenetic migration from the plume to the shelf. This indicates that the plume front is not a barrier to all larvae originating within the plume.

No exceptional densities of larvae were associated with the plume front. Instead, peaks in abundance for most taxa were observed in surface waters at stations at least 1km away from the plume front. These findings vary significantly from studies of riverine plumes (Govoni *et al.* 1989, Thorrold and McKinnon 1995, Kingsford and Suthers 1994), but are similar to studies in coastal systems where waters are influenced by tides or topography (Kiorboe *et al.* 1988, Taggart *et al.* 1989, Munk 1993). In the case of coastal fronts, a broader zone of aggregation developed because of the formation-breakup and reformation of fronts across a shoal. The larval patterns observed during the summer of 1994 are similar and suggest that tidal action, principally horizontal tidal oscillation of the front, drives the development of these multi-specific larval peaks.

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The mixed water mass seaward of the front observed on three of the four 1994 sampling dates suggests that physical processes within the baymouth and near coast may be important in affecting larval retention and subsequent recruitment By continually re-aggregating larvae in a frontal zone of mixed water either wind driven transport or the estuarine circulation may transport these retained larvae into the bay These observed patterns support a physical rather than biological explanation for the occurrence of shelf taxa inshore of the plume front, as well as for the presence of pre-flexion estuarine spawned taxa (*Anchoa* spp) in shelf waters

On a larger scale (7 5 km), two larval assemblages reflecting plume and shelf waters were found The two assemblages compared favorably with the assemblages derived by Olney (1996), with the noted absence of *M. undulatus* and the placement of *Symphurus* spp within the plume assemblage No larval aggregation was observed within a broad frontal zone defined by moderate chl-a concentrations during the summer of 1992 When these findings are compared with the findings during 1994 (chap 3) the results suggest that aggregation is scale dependent

Studies that have focused on riverine plumes have found that the frontal zone was many kilometers wide and supported enhanced chl-a concentrations (Richardson 1973, Lohrenz et al 1990, Grimes and Finucane 1991) These studies have hypothesized that higher primary production within the frontal zone would result in increased growth and survival of larvae aggregated within the broad frontal zone The lack of enhanced chl-a concentrations along with moderate larval densities within the frontal zone defined by chl-a in this study, suggest that larvae within the frontal zone may not gain an energetic advantage over other larvae found elsewhere on the shelf

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Wind-driven coastal upwelling was an important factor controlling the distribution of larvae on a broad scale (15 km) during August 1988. Coastal upwelling transported plume water and significant numbers of plume and near-coastal taxa to the mid-shelf in just a few days. Although it is generally believed that export away from juvenile habitats leads to death (Hjort 1914), little information on the survival of larvae transported to the shelf is available. Some taxa like the Blue crab, (*Callinectes sapidus*) export their larvae to the shelf where they develop. A combination of physical factors including a wind driven coastal counter-current (northward flowing) followed by onshore wind transport, are responsible for determining post-larval recruitment (Johnson and Hester 1989). For taxa like *Anchoa* spp. that are transported to the shelf in plume waters during these upwelling events, mortality due to advection may not be certain. Transport of larvae to estuaries north of the baymouth may occur during such periods providing a mechanism for genetic exchange between estuaries along the coast.

The sub-surface transport of shelf waters to the coast during upwelling has obvious implications for larval transport to the estuaries. Larvae entrained into sub-surface waters as the plume flows out over the shelf during upwelling will be passively transported to the estuary. Such transport on the inner-shelf has been documented for pre-flexion sciaenid larvae, that were presumed to be *M. undulatus* (Olney 1996). It is therefore critical to assess the number and intensity of these events in order to fully understand the

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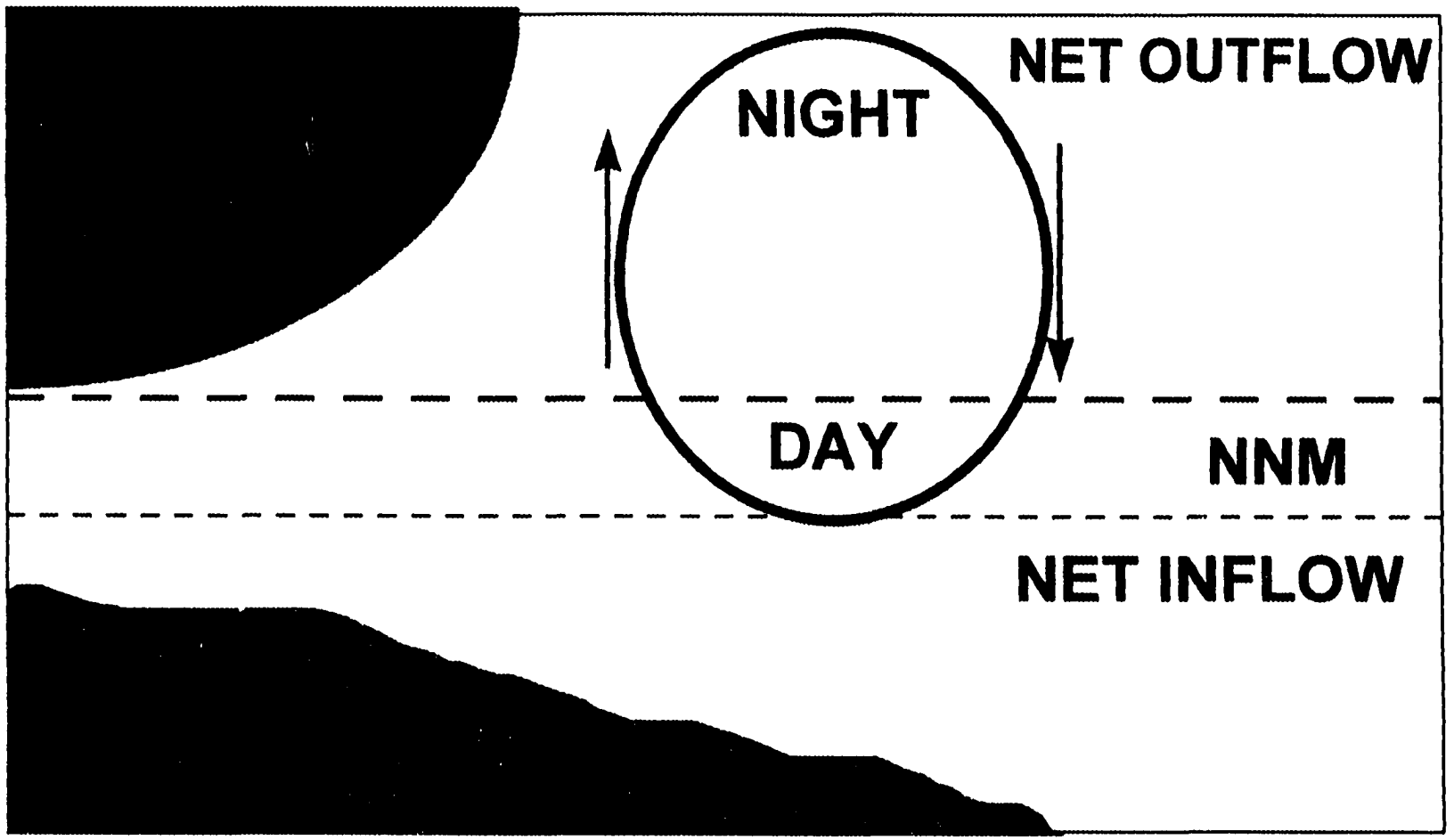

Figure 45 Conceptual model of shelf retention for *Etropus microstomus* Vertical migration to layer of no net motion (NNM) at the pycnocline occurs during the day Dispersal or migration into the surface waters where net flow is offshore occurs at night (Modified from Cho 1996)

transport potential, and their importance as regulators of recruitment success

The Richardson number, the ratio between buoyancy and inertia in the water column, may be a useful parameter to determine when offshore transport may occur Kourafalou *et al.* (1996a, 1996b) has used the Richardson number to determine under what conditions the coastal plume of the SAB would be transported to the shelf A similar formulation, modified for the MAB and the Chesapeake Bay, could be used to forecast when cross shelf transport of the Chesapeake Bay Plume should be expected, so that appropriate spatial and temporal sampling of the mesoscale oceanography in the vicinity of the baymouth can be conducted. Such samples are necessary to understand the influence of the mesoscale oceanography on recruitment and larval survival.

Vertical distribution

Behavior of larvae is a critical component of larval recruitment and may act to maintain distinct larval assemblages (Crisp 1974, Boehlert and Munday 1988) The plume and shelf taxa examined during the summer of 1992 exhibited a variety of vertical distributions that, in some cases, varied dielly A strong diel change in vertical distribution was found for the shelf indicator taxa *E. microstomus* The hypothesized vertical migratory pattern of *E. microstomus*, as described from the changes in vertical distribution, places larvae deeper in the water column near the pycnocline during the day, and then places these larvae in waters above the pycnocline at night Cho (1996) found a similar diel pattern for *E. microstomus* larvae collected off Long Island He hypothesized that such a distribution retained larvae within the shelf This should minimize shoreward transport because water velocities are minimal at the pycnocline Movement into the water column at night will place the larvae into waters with a net offshore transport (Fig 45)

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Such a behavior is simple tidal stream transport operating in reverse and has been described for some decapod larvae whose larvae are retained in offshore shelf waters (Maris 1986).

Recruitment Strategy of M. undulatus

Spawning, development and recruitment patterns for *M. undulatus* in the Middle-Atlantic Bight has been described by Norcross and Austin (1988). The early life history of this taxa is composed of larval development on the shelf and recruitment to estuaries. According to Norcross (1983), spawning takes place during fall (peaking in late September and October) on the continental shelf delineated by water of at least 16 °C. Spawning progresses offshore through the season as water temperatures nearshore cool. Larvae develop in offshore waters, where a combination of onshore wind transport and an ontogenetic migration (to depth) are thought to determine recruitment to the estuary (Norcross 1991). Norcross (1983) found a correlation between the best 40 days of onshore (northeasterly) wind stress and year-class-strength. She correlated the "best onshore wind" with the cessation of summer winds (southwesterly) during late August or early September in the MAB. Her correlations have not held, and this suggests that other factors may influence year-class-strength.

The Chesapeake Bay plume front is a likely feature that can affect survival and recruitment because of its broad scale, and influence on the spatial distribution of ichthyoplankton. The smallest Atlantic croaker larvae (< 3.5 mm) were most abundant just outside the baymouth where warm water is found throughout the summer (except during upwelling) (chap. 3). Additionally, larvae were collected as early as the first week of August, which traditionally is the season of strongest upwelling favorable winds (Johnson

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and Hester 1989). Other studies, (Barbieri *et al* 1993) have found evidence of spawned out *M. undulatus*, as early as July. Since larvae are abundant within the baymouth as early as August, frontal dynamics within the baymouth and nearshore may retain larvae near the coast where tidal currents, estuarine circulation, and ontogenetic migration can facilitate transport into the estuary. This would not require a strong wind driven transport component to drive recruitment early in the season.

The difference between the recruitment strategy proposed by Norcross (1983, 1991) and the hypothesis presented here is subtle, but suggests that in order to understand and predict recruitment of this taxa, behavior, mesoscale physical oceanographic processes, and climatic events should be integrated in any model. Further, understanding how survival differs between early-spawned and late-spawned larvae once they enter the rivers may elucidate which group of larvae are likely to contribute most to year-class-strength of this taxa.

Future Studies

Aside from the studies that have been described in the previous sections, there are several other studies that are necessary to understand how the plume affects larval distributions, survival, and recruitment. First, time-series measurements of larval abundance, current velocity, and hydrographic properties at varying distances from the baymouth should be conducted. These studies should be of sufficient length in order to resolve both tidal and diel migrations, and any changes related to distance from the baymouth. This type of study has been successfully used to describe retention, aggregation and recruitment of larval shrimp *Penaeus plebejus* (Rothlisberg *et al* 1989) as well as many decapod crustaceans (Maris 1986), and may therefore provide a suitable bio-

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physical explanation for larval recruitment of sciaenids to estuaries like the Chesapeake Bay.

The dispersal potential of larvae transported offshore is unknown, as is the degree of connectivity between estuaries north and south of the Chesapeake Bay. The physics of the plume may prove to be an important factor. Techniques now exist to document the elemental composition of the primordia of the otoliths of fish. This elemental signature could be used to document the origin of larvae found on the shelf. Studies that integrate physical observations of plume location and transport along with such chemical techniques could reveal how populations north and south of the bay may be connected.

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Appendix A

Spearmans rank correlation matrices for summer 1994

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Table 1. Spearmans correlations between taxa and environmental parameters at 1m, July 5, 1994. Bonferroni adjustment for multiple comparisons is used to adjust α. The resulting significance level is 0.006. The upper number in the matrix is the r-value and the lower number is the significance (p). Significant correlation's and their respective probabilities are highlighted in bold.

	Anchoa spp.	*Symphurus* spp.	*Menticirrhus* spp.	*Etropus microstomus*
Anchoa spp.	1	0.26098	-0.32005	-0.52223
	0	0.4664	0.3673	0.1215
Symphurus spp	0.26098	1	0.06386	-0.21418
	0.4664	0	0.8609	0.5524
Menticirrhus spp	-0.32005	0.06386	1	-0.16563
	0.3673	0.8609	0	0.6475
Etropus microstomus	-0.52223	-0.21418	-0.16563	1
	0.1215	0.5524	0.6475	0
Salinity 1m	-0.58788	-0.35046	0.52765	0.52223
	0.0739	0.3208	0.117	0.1215
Chlorophyll-a	0.61212	0.14168	-0.4152	-0.52223
	0.06	0.6962	0.2328	0.1215
Frontal Distance	**-0.80606**	-0.1715	0.52765	0.52223
	0.0049	0.6357	0.117	0.1215
Bulk Stratification	0.06667	0.21624	-0.33735	-0.40618
	0.8546	0.5485	0.3405	0.2441

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Table 2 Spearmans correlations between taxa and environmental parameters at 1m, August 9, 1994. Bonferroni adjustment for multiple comparisons is used to adjust α. The resulting significance level is 0.006. The upper number in the matrix is the r-value and the lower number is the significance (p). Significant correlation's and their respective probabilities are highlighted in bold.

	***Anchoa* spp**	***Symphurus* spp**	***Menticirrhus* spp**	***Micropogonias undulatus***	*Etropus microstomus*
***Anchoa* spp**	1	-0.00769	0.78901	0.17961	0.14426
	0	0.9832	0.0067	0.6195	0.6909
***Symphurus* spp**	-0.00769	1	0.15121	0.64253	0.32161
	0.9832	0	0.6767	0.0451	0.3648
***Menticirrhus* spp**	0.78901	0.15121	1	0.58835	0.38695
	0.0067	0.6767	0	0.0736	0.2693
Micropogonias undulatus	0.17961	0.64253	0.58835	1	0.52382
	0.6195	0.0451	0.0736	0	0.1202
Etropus microstomus	0.14426	0.32161	0.38695	0.52382	1
	0.6909	0.3648	0.2693	0.1202	0
Salinity 1m	-0.73161	-0.1715	-0.61451	-0.17408	-0.231
	0.0162	0.6357	0.0587	0.6305	0.5208
Chlorophyll-a	0.79672	0.21783	0.54772	0.13693	0.35147
	0.0102	0.5734	0.1269	0.7254	0.3537
Frontal Distance	-0.73161	-0.29081	-0.61451	-0.17408	-0.20669
	0.0162	0.415	0.0587	0.6305	0.5667
Bulk Stratification	0.32516	0.14168	0.13656	0.05803	-0.07295
	0.3593	0.6962	0.7068	0.8735	0.8413

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Table 3 Spearmans correlations between taxa and environmental parameters at 3m, August 9, 1994. Bonferroni adjustment for multiple comparisons is used to adjust α. The resulting significance level is 0.006. The upper number in the matrix is the r-value and the lower number is the significance (p). Significant correlation's and their respective probabilities are highlighted in bold.

	Anchoa spp.	*Symphurus* spp.	*Menticirrhus* spp	*Micropogonias undulatus*	*Etropus microstomus*
Anchoa spp	1	0.51818	0.93439	-0.03636	0.05681
	0	0.153	0.0002	0.926	0.8846
Symphurus spp	0.51818	1	0.67696	0.21818	-0.05244
	0.153	0	0.0452	0.5728	0.8934
Menticirrhus spp	0.93439	0.67696	1	0.0286	0.11
	0.0002	0.0452	0	0.9418	0.7781
Micropogonias undulatus	-0.03636	0.21818	0.0286	1	-0.07866
	0.926	0.5728	0.9418	0	0.8406
Etropus microstomus	0.05681	-0.05244	0.11	-0.07866	1
	0.8846	0.8934	0.7781	0.8406	0
Salinity 3m	-0.6789	-0.68761	-0.8581	-0.20019	0.10042
	0.0443	0.0407	0.0031	0.6056	0.7971
Chlorophyll-a	0.80512	0.65873	0.91322	0.21562	0.15569
	0.0159	0.0757	0.0015	0.6081	0.7128
Frontal Distance	-0.6789	-0.64409	-0.8581	-0.20019	0.06695
	0.0443	0.0612	0.0031	0.6506	0.8641
Bulk Stratification	0.33075	0.49612	0.52947	-0.12185	0.35147
	0.3846	0.1743	0.1427	0.7548	0.3537

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Table 4. Spearmans correlations between taxa and environmental parameters at 1m, September 7, 1994. Bonferroni adjustment for multiple comparisons is used to adjust α. The resulting significance level is 0.006. The upper number in the matrix is the r-value and the lower number is the significance (p). Significant correlation's and their respective probabilities are highlighted in bold.

	Anchoa spp.	*Symphurus* spp.	*Menticirrhus* spp.	*Micropogonias undulatus*	*Etropus microstomus*
Anchoa spp.	1	0.08547	0.39841	-0.10445	0.21408
	0	0.7813	0.1775	0.7342	0.4825
Symphurus spp.	0.08547	1	0.05976	0.07189	-0.23039
	0.7813	0	0.8462	0.8155	0.4489
Menticirrhus spp.	0.39841	0.05976	1	0.46721	0.06355
	0.1775	0.8462	0	0.1075	0.8366
Micropogonias undulatus	-0.10445	0.07189	0.46721	1	0.35545
	0.7342	0.8155	0.1075	0	0.2333
Etropus microstomus	0.21408	-0.23039	0.06355	0.35545	1
	0.4825	0.4489	0.8366	0.2333	0
Salinity 1m	-0.49577	-0.26207	-0.28504	0.19217	0.57219
	0.0849	0.3871	0.3452	0.5294	0.041
Chlorophyll-a	0.4898	0.26207	0.37901	0.0113	-0.56476
	0.0893	0.3871	0.2015	0.9708	0.0443
Frontal Distance	-0.44799	-0.26207	-0.33203	0.13565	0.66137
	0.1247	0.3871	0.2677	0.6586	0.0138
Bulk Stratification	0.55029	0.34991	0.09253	-0.17828	-0.35346
	0.0513	0.2412	0.7637	0.5601	0.2361

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Table 5. Spearmans correlations between taxa and environmental parameters at 3m, September 7, 1994. Bonferroni adjustment for multiple comparisons is used to adjust α. The resulting significance level is 0.006. The upper number in the matrix is the r-value and the lower number is the significance (p). Significant correlation's and their respective probabilities are highlighted in bold.

	Anchoa spp.	*Symphurus* spp.	*Menticirrhus* spp.	*Micropogonias undulatus*	*Etropus microstomus*
***Anchoa* spp**	1	-0.63509	0.24772	-0.20184	0.18312
	0	0.0358	0.4627	0.5517	0.5899
***Symphurus* spp**	-0.63509	1	0.25743	0.10488	-0.405
	0.0358	0	0.4447	0.7589	0.2166
***Menticirrhus* spp**	0.24772	0.25743	1	0.18182	-0.18144
	0.4627	0.4447	0	0.5926	0.5934
Micropogonias undulatus	-0.20184	0.10488	0.18182	1	0.71647
	0.5517	0.7589	0.5926	0	0.0131
Etropus microstomus	0.18312	-0.405	-0.18144	0.71647	1
	0.5899	0.2166	0.5934	0.0131	0
Salinity 3m	-0.10092	-0.31464	-0.40909	0.66364	**0.81883**
	0.7678	0.346	0.2115	0.026	**0.0021**
Chlorophyll-a	0	0.40999	0.47273	-0.46364	**-0.80022**
	1	0.2104	0.142	0.1509	**0.0031**
Frontal Distance	-0.09175	-0.31464	-0.5	0.53636	**0.85605**
	0.7885	0.346	0.1173	0.089	**0.0008**
Bulk Stratification	-0.0367	0.42906	0.01818	-0.6	-0.60481
	0.9147	0.1879	0.9577	0.051	0.0487

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Table 6. Spearmans correlations between taxa and environmental parameters at 1m, September 20, 1994. Bonferroni adjustment for multiple comparisons is used to adjust α. The resulting significance level is 0.006. The upper number in the matrix is the r-value and the lower number is the significance (p). Significant correlation's and their respective probabilities are highlighted in bold.

	Anchoa spp.	*Symphurus* spp.	*Menticirrhus* spp	*Micropogonias undulatus*	*Etropus microstomus*
Anchoa spp.	1	0.57911	-0.1	0.4	-0.10092
	0	0.0619	0.7699	0.2229	0.7678
Symphurus spp.	0.57911	1	0.23164	0.38958	0.01063
	0.0619	0	0.4931	0.2363	0.9753
Menticirrhus spp	-0.1	0.23164	1	0.1	0.10092
	0.7699	0.4931	0	0.7699	0.7678
Micropogonias undulatus	0.4	0.38958	0.1	1	0.49543
	0.2229	0.2363	0.7699	0	0.1212
Etropus microstomus	-0.10092	0.01063	0.10092	0.49543	1
	0.7678	0.9753	0.7678	0.1212	0
Salinity 1m	-0.40183	**-0.79331**	-0.10046	-0.11872	0.12903
	0.2206	**0.0036**	0.7688	0.7281	0.7053
Chlorophyll-a	0.40183	0.62407	0	-0.17808	-0.58526
	0.2206	0.0402	1	0.6004	0.0586
Frontal Distance	-0.40091	-0.62264	0	0.18223	0.50576
	0.2217	0.0408	1	0.5918	0.1125
Bulk Stratification	0.40091	0.30604	-0.30068	0.13667	0.0092
	0.2217	0.36	0.3689	0.6886	0.9786

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Table 7 Spearmans correlations between taxa and environmental parameters at 3m, September 20, 1994. Bonferroni adjustment for multiple comparisons is used to adjust α. The resulting significance level is 0.006. The upper number in the matrix is the r-value and the lower number is the significance (p). Significant correlation's and their respective probabilities are highlighted in bold.

	Anchoa spp.	*Symphurus* spp.	*Menticirrhus* spp.	*Micropogonias undulatus*	*Etropus microstomus*
Anchoa spp	1	-0.3	-0.41781	-0.54772	-0.54772
	0	0.4328	0.2631	0.1269	0.1269
Symphurus spp	-0.3	1	**0.92848**	0.63901	-0.14606
	0.4328	0	**0.0003**	0.0639	0.7077
Menticirrhus spp	-0.41781	**0.92848**	1	0.83063	0.13561
	0.2631	**0.0003**	0	0.0056	0.7279
Micropogonias undulatus	-0.54772	0.63901	0.83063	1	0.36667
	0.1269	0.0639	0.0056	0	0.3317
Etropus microstomus	-0.54772	-0.14606	0.13561	0.36667	1
	0.1269	0.7077	0.7279	0.3317	0
Salinity 3m	-0.54772	-0.56598	-0.40684	-0.08333	0.61667
	0.1269	0.1122	0.2772	0.8312	0.0769
Chlorophyll-a	0.55002	0.43085	0.33194	0.17573	-0.5272
	0.125	0.247	0.3828	0.6511	0.1447
Frontal Distance	-0.54772	-0.56598	-0.40684	-0.08333	0.61667
	0.1269	0.1122	0.2772	0.8312	0.0769
Bulk Stratification	0.54772	-0.23735	-0.20342	-0.08333	-0.26667
	0.1269	0.5386	0.5996	0.8312	0.4879

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MANUSCRIPTS

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